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104 SOUTH FIFTH STREET
1937

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PROCEEDINGS
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**THE TEXT OF ACTS IN MS 146 OF THE
UNIVERSITY OF MICHIGAN**

HENRY A. SANDERS AND JOHANNA OGDEN

(Read April 24, 1936)

ABSTRACT

This is a manuscript of 210 leaves made up of various parts. Seventy-eight leaves contain a text and commentary of Acts, written in the twelfth century. The text is in a narrow column in the middle of each page, while the commentary fills a like column on each side. The commentary contains much from Bede and Rhabanus Maurus. There are also interlinear glosses of a different character mixed with the text.

In text this manuscript has 1384 variants from the Wordsworth and White Vulgate text, of which 756 are important, being classified as 206 additions, 93 omissions, 128 differences in order, 201 word changes, and 128 changes in construction. In 234 cases these variants find support in the Sixtine and Clementine editions and less frequently in old Vulgate manuscripts, especially those having Irish or English text. There is therefore a strong probability that the majority of the agreements with the Sixtine-Clementine editions come from a similar source, that is, an Old Latin text antedating the Vulgate. As this text disagrees with each of the known Old Latin texts almost as often as it agrees, it probably derives from a different Old Latin base, presumably Irish-English. This hypothesis is strongly supported by the following facts: 181 of these variants are supported by the Western text (Codex Bezae, African Old Latin, etc.) of which less than one third are found in the Sixtine-Clementine editions; 320 are supported by the European Old Latin, of which only one third are found in Vulgate editions or manuscripts; there are 180 other readings in MS 146, which are of similar type to the above, but which are not supported by any known edition or manuscript. Origin from an Irish Old Latin base seems the best explanation for these numerous and remarkable variants.

DESCRIPTION OF THE MANUSCRIPT

MS 146 of the library of the University of Michigan is a combination containing the Acts of the Apostles, the Apoca-

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lypse, the Catholic Epistles and some other material. The Bible text is abundantly supplied with marginal and inter-linear commentary. As this article deals only with the text of Acts, I shall disregard the remaining parts except in so far as it may be necessary to discuss matters connected with the history of the manuscript

The whole manuscript consists of 210 leaves of parchment, measuring approximately 22 cm. in height and 17 cm. in width. Of these only nine quires of eight leaves each and one of six leaves were in the original Acts manuscript.

All of these were ruled, with a brown pencil, for sixteen lines of text in the middle of each page and with two perpendiculars about 2 or 3 mm. apart to mark the beginnings and ends of the lines. Two other perpendiculars were also ruled 1 cm. or more from each edge of the leaf to mark off two narrow columns for the commentary. Lines for the commentary were ruled as needed later.

The text and commentary of Acts are by different scribes, but contemporary. Spaces were left for the initial letters to be put in by the rubricator, the letter of small size being written on the left margin. Sometimes these small letters have been cut away by later binders.

The writing is twelfth century and probably early twelfth. Green, as well as red, brown, and blue initials are frequent. Abbreviations are few, regular, and moderate in number in the text, but more numerous in the commentary. Words of one syllable frequently have a slanting stroke above. Double i has a slanting stroke above each i to distinguish ii from u. A slanting stroke was used for a hyphen regularly at the end of a line when a word was divided. Punctuation is a single dot in middle or low position and the question mark (ʒ). Tall s (ſ) is the regular form except that as initial, or rarely to begin a sentence not initialed, or at the end of a paragraph, round S is used.

Infrequent corrections are found from a contemporary hand, usually in a slightly paler ink. There are also some in a darker ink. Neither of these hands can be definitely dis-

tinguished from that of the scribe of the commentary. On pages 66 to 69 very extensive additions were made both in the margins and between the lines. This hand is also very similar and the ink is a lighter brown. The writing is certainly practically contemporary, so it seems best to assign all these corrections and additions to the diorthotes, but not to press his identity with either of the original scribes of the manuscript. No Arabic numerals appear in first or second hands. Running titles at tops of pages, chapter divisions, and numbers, are all by later hands.

Pages 156 to 158 of the manuscript were left blank. Later these pages were filled with a collection of maxims drawn from various Fathers, the first being: "Isidorus. Ante factum cogita diu, ante opus praemeditare diu, quod vis agere, diu exquire, diu proba, et sic facias, cum diu cogitaveris; tunc fac quod probaveris." The collection proved too long for the three pages, though the writing was crowded and the number of lines greatly increased, there are 45 on the first two pages and 49 on the third. So another leaf was inserted and 54 lines written on its first side, but the other side, which rubbed against the cover, was left blank. This extra leaf was cut with the inner corners clipped off, so as to reduce the length of the binding edge from 22 cm to 10½ cm. It is possible that this was done so that the extra leaf could be inserted in a book already bound.

The maxims, though written in a hand of the same school as the manuscript of Acts, are certainly not by the same scribe, nor with the same ink or pen. The text of Acts was written with a blacker ink and a coarser pen, the commentary, both marginal and interlinear, was in a brownish ink and written with a finer pen point. The maxims in both respects take an intermediate position. The forms of the letters are similar, but note that capital N (N), common in Acts, is always replaced by the enlarged minuscule Ń. Also, the use of abbreviations has greatly increased and not all are as obvious as in the text and commentary of Acts. Furthermore, the punctuation has changed, so that the dot in lowest

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position is regular, and (?) is rarely used for comma or semicolon. While these pages were written later than Acts, and probably considerably later, they are in a twelfth-century hand. *ii* is distinguished as in the rest of the manuscript, and single *i* is never so marked. The use of accent strokes over words of one syllable is more regular than in the rest of the manuscript.

The Apocalypse and Catholic Epistles were written in the thirteenth century, probably early in the century. We may note the frequent use of the stroke over single *i*, increased number of abbreviations, and more elaborate punctuation. The text is probably all by the same scribe, though he changed his pen and ink at times. Most of the commentary was written by a second scribe. A third scribe assisted, particularly in the middle portion.

The ten quires of the manuscript of Acts were originally numbered with Roman numerals at the bottom in the middle of the last page of each quire. Also *reclamantes* were added by the same hand. Most of these have been cut away, but quire numbers can be clearly read at the bottoms of pages 32, 64, 114, 130, and 146, *reclamantes* remain on pages 80, 114, 130, and 146. These were all eight-leaf quires except the tenth, which had originally six. A new numbering started in the Apocalypse-Catholic Epistles manuscript, of which the quires have ten or twelve leaves each. Of the quire numbers at the bottoms of the last pages only III on p. 220 and ·IIII at the bottom of p. 240 remain. *Reclamantes* are preserved on pp. 308, 328, 348, 368, 392.

There can be no question that there were originally two separate manuscripts. The parchment also is different in the two parts, being much thinner and whiter in the Apocalypse-Catholic Epistles portion. The coarse, stiff parchment of the Acts portion also points to an earlier date. The two manuscripts were bound up as one probably late in the thirteenth century. At the time of the binding or soon after a very uncouth scribe put in chapter numbers, both opposite the chapter beginnings and also in the lower margin, in Arabic

numerals preceded by C = *capitulum*. For chapters ten and twenty he used Roman numerals, perhaps because he knew no zero. All his figures are awkward in form but several are distinctive: 2 = 2, 4 = 4, 5 = 5, 6 = 6, and 7 = 7. I find no example of such a seven elsewhere, though Hill's tables show both \wedge and \vee for seven before the thirteenth century. This seems a cursive variation of the inverted form. The same hand wrote many additional notes in the margins, all in a very crude hand and with very pale ink. These are sometimes duplicated, probably from the same source, by a later hand.

Soon after the time of this scribe, another wrote in a beautiful, consistent hand, running titles and chapter numbers in Roman numerals at the tops of the pages and also added the chapter numbers following Ca(pitulu)m in the margins opposite the beginning of each chapter. Sometimes these are written over the Arabic numbers. This is a late thirteenth-century hand, but quite different from the hand that wrote the small leaf 55 (= pp. 99-100), and all of page 160, as well as short notes on pages 3, 4, 5, etc. of the Acts manuscript. The same scribe added many extra marginal and interlinear glosses in the Apocalypse-Catholic Epistles manuscript. The writing of this scribe is very similar to that of the third scribe of the Apocalypse-Catholic Epistles manuscript, but easily distinguishable by the shade of the ink, when both appear on the same page. We can not be sure whether these extensive additions were inserted before or after the rebinding, but it must have been about the same time. The hand is late thirteenth century, for in so many notes I failed to find a single instance of t with its top extending above its cross stroke.

Perhaps contemporary or nearly so to this corrector was a rubricator, who added alternately blue and red paragraph marks to each gloss in the last three chapters of the Apocalypse, in most of the Epistle of James and a few in I Peter.

About this time, and certainly not later than the early fourteenth century, a scribe corrected the Arabic numerals opposite the chapter beginnings and added them in the

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upper margin at the right hand corner of every other page. We may note the forms 7 = 2, e = 4, ¶ = 5 and Λ = 7.¹ These corrections are often written over the earlier Arabic numerals. A later binding cut away some of these on the upper margin, and they were rewritten somewhat lower. These later numbers have the modern form for 2 but retain e for 4, ¶ for 5, and Λ for 7. This fixes the date of this rebinding and renumbering as not later than the middle of the fifteenth century. Probably at the time of the first binding of the whole manuscript five blank parchment leaves were added at the beginning and two at the end. Certainly a hand approximately contemporary to that which put in the running titles and chapter numbers, but later than the writer of the marginal glosses, inserted on these blank pages certain titles with references to the places in the margins and glosses and text where the subjects were treated. These are as follows

carcer ma(rgo). Apo(calipsis) 2 e.
 color albus m(ar)g(o) Apo(calipsis) 1 d
 clavis . ma(rgo) . Apo(calipsis) 3 c
 diabolus im(m)o te(m)ptat glo(ssa) 1 Pe(tri) 5 . d
 docere im(m)o d(icit) glo(ssa) 1 . Pe(tri) . 4 . []
 gladi(us) ma(rgo) Ap(oc)a(lipsis) 2 e
 Im(m)o honorificam(us) d(eu)m . glo(ssa) 1 . Pe(tri) 4 d
 mulier co(n)ornat(us) de bonis et malis et ruinis . glo(ssa) 1 .
 Pe(tri) 3 a
 Om(n)e q(u)od e(st) i(n) mu(n)do . 1 Jo(hannes) . 2 . e .
 [.] 1 Pe(tri) 4 e
 parad(is)us ma(rgo) Apo(calipsis) 2 c .
 [] cedat i(n) o(mn)i obseq(u)o 1 Pe(tri) . 2 . e .

There are a few other notes and scribbles scattered through the manuscript, which it does not seem possible to classify, either with the hands just described or with a single scribe or time. All are negligible except one on page 2 giving a table of ten appearances of Christ after the resurrection, each with the correct New Testament reference. Number 10 was trimmed away at a later binding. This seems to be a

¹ Compare Thompson, *Greek and Latin Palaeography*, p. 92, and G. F. Hill in *Archæologia*, 62, 137 ff.

sixteenth- or seventeenth-century hand and would be of little importance had not the same scribe written this note on the first fly leaf: Ffranciscus . ma . le . me tenet Also, on leaf 6^r just above the commentary, the same hand wrote: Ffranciscus Smailes me tenet anno dni MDCXXIIII This fixes the date and makes sure that it is a person and not a monastery that is named as the owner ¹

Later the manuscript came into the possession of William Constable, Esq , F R S and F A S , and has his bookplate on the inside of the front cover He died in 1791 at Burton Constable in Holderness, County York, in his seventieth year. He had been elected a Fellow of the Royal Society on May 4, 1775. Perhaps the note N 23 on the last fly leaf was inserted for his library. William Constable bought the estate and library in Holderness, County York, from John Burton, who died in 1771 Therefore presumably MS 146 was in the Burton library before that date. Sir Talbot Clifford Constable sold the Burton-Constable library at auction in London, June 24-29, 1889 Ridler bought MS 146. The number A 723 and the price mark \$400 belonged to Voynich, from whom the University of Michigan Library obtained the manuscript on December 22, 1924, at a price of \$340.

A COMPARISON OF MS 146 WITH INDIVIDUAL VULGATE MANUSCRIPTS AND THE SIXTINE-CLEMENTINE EDITIONS

The purpose of making a comparative study of MS 146 with the other texts of the Acts is to determine the amount and character of its Old-Latin readings The Latin text of the Acts ² that was used at the time of Cyprian we know at

¹ This hand is extremely cursive and would have been most difficult to read with certainty if we had not had the long note on leaf 6^r (= p 2) just described Even with this aid the name caused difficulty Dr Richard Salomon first suggested to me the name Franciscus and Dr Robin Flower read the name as given above and suggested the identification with Francis Smayles, matriculated pensioner from St John's College, Cambridge, in 1614. He seems to have been a member of the Yorkshire family of that name

² For the history of the African Old-Latin text of the Acts cf Jülicher, *Zeit f d. Neutest. Wissenschaft*, XV, pp 163-188, P Capelle, *Le texte du psautier latin en Afrique* (Collectanea Biblica Latina cura et studio Monachorum S Benedicti), IV, Rome, 1913

least in part. The so-called European text is also known through several manuscripts, lectionaries, and patristic quotations,¹ and something is known of its relative, the Spanish Old-Latin,² but for the Acts the existence of an Irish Old-Latin text has not been proved.³




In comparing MS 146 with the Vulgate⁴ we find 1384 variant readings. There is no chapter in which the variants are exceptionally frequent, for in Chapter I there are 34 variants, in Chapter XXVIII, 47, and a number near these figures is found in the other chapters. The variations in order of frequency are spelling (628), additions (206), word-usage (201), word-order (128), syntax (128), omissions (93). The accompanying table will show the support of our manuscript by individual Vulgate manuscripts and the  editions in the different types of variants except spelling

TABLE I

MSS	Additions	Word-usage	Word-order	Syntax	Omissions	Totals
A	18	18	4	17	5	62
C	29	18	7	20	17	91
D	54	35	13	25	11	138
F	16	26	9	22	13	86
G	7	19	1	15	8	50
G ^o	19	6	0	5	2	32
I	13	22	3	19	9	66
T	34	23	5	25	17	104
V	42	40	11	32	14	139
Θ	38	29	4	23	8	102
Editions						
	69	52	34	57	22	234
	10	6	0	8	1	25
Ⓒ	0	0	0	2	0	2

¹ The best representative is the thirteenth-century MS Gigas at Stockholm.

² Berger, *Histoire de la Vulgate*, p. 8 et seq.; Jackson-Lake, *The Beginnings of Christianity*, III, The Text of Acts, p. cxxv, for Pacian's (A.D. 360-390) use of a Psalter akin to that of Cyprian, also *ibid.*, p. cxxxii for early African text in Spain.

³ The Irish Old-Latin for the Gospels is known through MSS r and r² among others. Cf. H. C. Hoskier, *Concerning the Genesis of the Versions of the New Testament*, I, p. 9 f.

⁴ Wordsworth and White, *Novum Testamentum Latine*, III, 1, Actus Apostolorum, 1905.

⁵ Old-English  and Ⓒ represent the Sixtine-Clementine Editions of the Bible.

Individual Vulgate manuscripts presumably show agreement with MS 146 against the Vulgate in proportion as they contain Old-Latin readings. From Table I it is noted that this support is found fairly equally in additions, word-usage, syntax, and omissions. Agreements in word-order are few except in D. D and V give the most support, with T, Θ, C, F, A, G, and G° following in the order named. This is a noteworthy observation, since D represents the best Irish tradition of the Vulgate and V the best of the ninth-century recension of Alcuin,¹ the greatest of the English scholars. It would seem then that our manuscript was derived from a very old text, either Irish in origin or related to the Irish, as it is supported frequently by these excellent manuscripts. A also was written in England in the seventh-eighth centuries, but was copied from an Italian manuscript. F² is an Italian manuscript that shows in general a relationship to A and V which is evidenced in the collation with MS 146. T is the best of the Spanish manuscripts, while Θ represents the edition of Theodulf, a Spaniard. There is some individual support found in C and G—G°, which represent other good families respectively of Spain and Southern Gaul.

In Table I in addition to the Vulgate manuscripts we have recorded the variant-support of our manuscript in the Sixtine-Clementine editions. There are 234 variant-agreements in which **BC** both give support, while **B** gives support alone in 10 additions, 8 instances of syntactical difference, 6 of word-usage, and 1 omission, **C** gives support alone only in 2 grammatical variants. For all except 105 of these variant-agreements there is also Western or European Latin support.

Our interest in **BC** is in the possibility of determining Old-Latin in the support given our manuscript. The sources of **BC** are not definitely known, but we assume that they were based upon manuscript authority. An examination of

¹ Cf S. Berger, *Histoire de la Vulgate*, pp. 37-40, for the history of Codex A and other codices of the Vulgate.

² Wordsworth and White, *op. cit.*, I, p. xii, Codex F is in agreement with A in the Gospels, V and F agree in the NT except for the Gospels and there Codices V and A agree. Jackson-Lake, *op. cit.*, p. cxxx, V in Acts I and II follows A rather than the Alcuinian text.

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these variants agreeing with **BC** shows recognized Old-Latin support for 129 of the 234 variants. There is also Old-Latin support for 48 of the variants supported by MS A, for 103 of those supported by D, and a similar proportion in the case of the other Vulgate manuscripts.

TABLE II
SOLE SUPPORT FOR MS 146 IN OLDER VULGATE MANUSCRIPTS

	Additions	Word-usage	Word-order	Syntax	Omissions	Totals
A	0	0	0	0	1	1
C	0	0	1	0	0	1
D	3	6	1	2	1	13
F	0	0	0	1	0	1
G ^o	2	0	0	0	0	2
I	1	0	0	0	1	2
T	1	0	0	0	0	1
Θ	0	0	0	1	0	1

Because of the noteworthy amount of Old-Latin support recorded in the agreement of Vulgate manuscripts and editions with our manuscript, in the number of instances of sole support there should be indication of Old-Latin influence. This appears to be of an Irish type, at least in part, because of the special agreements with MS D.

Many of the variants of MS 146, which are supported by **BC**, are known Old-Latin readings and others may be, but the reason for this relationship is not known¹ To MSS D and A of the Vulgate the relationship may be due to the fact that they issued from Ireland and England and that our manuscript is Irish-English, but this explanation does not suffice for the other Vulgate manuscripts.

The picture of the agreements of MS 146 with the older Vulgate manuscripts is not complete without a comparison with the known families of Vulgate manuscripts. When two or more manuscripts of a family agree, I list it as a family agreement. W. and W. list MS W alone as representing the

¹The Irish-English monks in the sixth to ninth centuries were founding and visiting monasteries in Western Europe and the influence of their Biblical text would appear in the manuscripts they studied and copied. Cf. Jackson-Lake, *op. cit.*, p. cxxxiii, Berger, *Histoire de la Vulgate*, Chapters III and IV

thirteenth-century type, but it is an English manuscript only a century later than MS 146. The remarkable agreement with W in non-Vulgate readings is enhanced by the cases where W furnishes the sole support: 3 additions, 3 cases of

TABLE III

Families	Additions	Word-usage	Word-order	Grammatical	Omissions	Total
GCAF D	31	35	8	29	15	118
I M S U T O	53	57	12	35	20	177
Θ KBVR	43	42	10	33	17	145
W	64	77	19	63	27	250

word-usage, 4 of word-order, and 4 grammatical variants, a total of 14. W is an English manuscript and so represents a corruption of the Vulgate more or less peculiar to England, yet we may accept the verdict of W and W, that it represents the current text of the time, at least in England

Family 1 suffers especially in this comparison because most of the non-Vulgate agreements of its manuscripts with MS 146 are individual, D with its 138 agreements being the most individual. There was evidently no influence of a Vulgate text of this type on any ancestor of MS 146. Family 2 comes off much better in the comparison, partly because the variants of two manuscripts in each of the groups making up the family are listed, but more because the older form of the Spanish text is here included, which we shall see later was most closely associated with the European Old-Latin. A partial revision of some ancestor of MS 146 to this type of Vulgate text is a possibility, but cannot be definitely affirmed. The agreements with family 3 are practically always agreements with KBVR. The number 145 is impressive until we note that there is only one case of sole support, a word-usage,

and that either W or representatives of family 2, or both, are always in agreement. There is no indication of a revision of the text of MS 146 to this Vulgate type.

The remarkable number of agreements, the date, and the place of origin, all point to a definite influence of the W type of Vulgate text on MS 146. It is not likely that MS 146 represents an edition or even a scholarly revision. There are too many conflate readings which are either ungrammatical or even unintelligible. For these compare the additions. 4.19 *ad eos dixerunt ad eos*, 4.32 *eorum ex his*; 10.29 *ergo ego*, man 1, 11.5 *vas quoddam vas*, 13.35, *ait dicit*; 20.7 *protextit protraxitque*, man 1, 20.9 *sublatus oblatus*, and 24.26 *enim autem* man 1

Proofs of the conflate character of readings are less apparent in other types of variants, yet a few have been noted, as 28.15 *tribus tabernas*, man 1. The most natural explanation for these errors is that an ancestor was corrected to a Vulgate type of text but the original reading was not in all cases deleted. A methodical but ignorant scribe then copied both readings or parts of both readings. As such errors are easily discoverable and are therefore apt to be removed as soon as discovered, this revision probably was made on the immediate parent of MS 146.

In the following tables showing agreements between MS 146 and the different Old-Latin texts, the full authority for each reading, including all Vulgate manuscripts cited by W and W, is given the first time it is cited. The large number of variants for which no Vulgate support, or only sporadic agreements, are cited definitely separates MS 146 from all of the families of Vulgate manuscripts, though most of these contain an appreciable Old-Latin element.

MS 146 AND THE WESTERN TEXT OF THE ACTS

The variants in MS 146 that are supported by the Old-Latin of the *Western Text* are:

1.4 add *inquit* after *audistis* Aug D Perp^o vg^{ss} c demid H1
Lat(CD G³ I M O R S³ T U W)

*11 order = *in celum a vobis* Aug

- 15 om. *et* d Perp* vg^{ss} Lat(A C I K M R T V W)
- 17 *qui* for *quia* Aug d c t demid Perp Gig vg^{ss} Lat(A* C D M T W)
- 20 *eius* for *eorum* Aug Ir Perp d^o(= D) demid lux cor vat* Lat(A C D Θ G M O R¹ S T U) and all Greek codd
inhabitet for *habitet* Aug D d c e Gig Ir Lat(A F G Θ M U V)
- *2.1 *implerentur* for *complerentur* d
- 4 *variis* for *aliis* Aug Perp Syr Petil c t cor vat^{ms} Amb Vict Vig Lat(A D Θ I M T V W)
- 8 *linguam nostram* for *lingua nostra* D Perp² vg^{ss} demid c cor vat Lat(B C D G Θ M O R T U W)
- 9 om *et* after *Mesopotamiam* D d Aug Ir Perp Gig c demid t vg^{ss} Lat(A^o M W)
- 13 *irridebant dicentes* for *inridentes dicebant* D d Aug Gig (Clark, not W and W) Syr
- 14 *elevavit* for *levavit* d Aug Perp c t alb arg Lat(B C F K O R S T W)
- 22 *nobis* for *vobis* D d Euseb Greek min(489 547* 1518 1831 1919) Lat(D)
- 29 om *et* after *quoniam* d Ir Perp Gig c demid Lat(B D F Θ K R S U W)
- 32 *nos omnes* for *omnes nos* d c Ir Gig Perp Syr Aug Lat(C T V)
- 38 add *domini* before *Iesu Christi* Cypr Perp (dñi nri) D d c E e Lucif Aug Amb Vig Lat(A) Greek min(614 etc) Sah Syr Arm Bas Cyr Thdrt
order = *spiritus sancti* Ir Cypr Gig Perp vg^{ss} Boh Sah c t demid Lat(Θ R)
- 40 *plurimis* for *pluribus* Aug e Perp vg^{ss} Lat(A I M O V)
- 41 order = *in die illa* Harcl(text) e vg^{ss} Vig Lat(W) all Greek except D
- 3.7 *manu eius* for *eius manu* Cypr h (Gig) Lucif (Perp) c vg^{ss} Lat(C F T)
- 11 *viderunt* for *tenerent* D(= *viderent*) vg^o (*videret*) Lat(D W) cor vat^{ms}

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- 12 *potestate* for *pietate* h Perp³ vg^{oo} Lat(W) Pesh Arm
 16 *vidistis* for *videtis* d vg^o lux Lat(I)
 19 *peccata vestra* for *vestra peccata* Ir Lat(C D T) Perp
 Gig lux m (Tert) D d h and Greek (≠ C P etc)
 21 om. *quidem* h Lat(M) Tert, Ir vg^{oo} transpose
 25 *nostros* for *vestros* after *pater* Ir D d h Perp Gig
 Lat(A C D K M R T V W) Greek (≠* C P 1 13 31
 al) vg^{oo}
 4.32 *cor unum* for *cor* Harcl Gig Perp Syr Sah Hil Arm
 Eth (Or) Aug Gaud c demid cor vat Lat(D W)
 33 order = *domini nostri iesu christi* D d E e Arm Eth,
 which om *nostri*, Perp + *nostri* with vg^{oo} Lat(Θ);
 Greek (B P al) Sah which om. *nostri* and *Christi*
 5.7 *eius* for *ipsius* d c Perp Gig Lucif Lat(A C G M T)
 = Greek
 9 add *dixit* Harcl (Gig) Perp E e Greek (A P S etc) Sah
 (= *ait*) Lat(D Θ R T) c
 10 *eam* for *illam* d e Gig
 15 *in plateis* for *in plateas* d e Perp Gig Lucif demid
 Lat(A B¹ M O S U W)
 illorum for *eorum* d c vg^{oo} Lat(V W)
 add *et liberarentur ab infirmitatibus suis* after *eorum*
 D d E e Gig Perp Lucif vg^{oo} Lat(M R³)(A D O) c
 demid
 16 om *et* after *autem* D d Lucif Gig Lat(D S T)
 36 order = *numerus virorum* D (d) h Gig Lat(A D) Perp
 vg^{oo} Chr Greek (H P min)
 *6.2 *vos* for *nos* h (*placet vobis*)
 3 add *sancto* after *spiritu* c e t h Lat(B D K R S T U
 V W) Greek (A C H P S min) vg^{oo} demid Sah Aeth
 Bas
 4 order = *erimus instantes* Harcl Gig (*adseruientes*); cf.
 D^o t Syr Chr Or
 7 *domini* for *Dei* D d Harcl E e c h vg^{oo} Lat(B F I¹ K R
 S U V W) Perp t Greek (431 614)
 13 *dicentes* for *qui dicerent* d c e demid g² Gig Perp lux^{*}
 Lat(B C D F Θ K O R S T U V W)
 15 add *in* before *eum* d Perp Gig e g² Lat(D O)

- 7 2 *moreretur* for *moraretur* = d (*mortuus esset*) Perp³ Gig
(*mortuus esset pater eius*)
- 5 *set* for *et*² D d Gig vg⁹⁰ c demid Lat(A D Θ I M R W)
Eth
- 6 add *ei* before *deus* vg⁹⁰ Gig c demid cor vat Lat(C I^o R
S T U* W) = (*Deus ad eum*) D d Ir
- 7 *dicat dominus* for *dixit Deus* d c Ir Perp demid Lat(M R¹
W), *dixit dominus* Gig vg⁹⁰ Lat(A C Θ¹ I O V)
deservient for *servient* d e Gig Perp c demid Lat(A C D
G Θ I M O R² T U*)
- 11 *super* for *in* D d E e all Greek
- 13 *manifestum* for *manifestatum* d e Lat(W)
- 22 om. *in* before *operibus* D d Perp Gig e Greek (≠ A B C
H al⁴⁰) Chr Ps—Just
- 24 add *de genere suo* after *iniuriam* D d E Gig Syr Harcl
Aeth
- 25 add *suos* after *fratres* d e Perp c Lat(M R² T), D
= Greek (A F H P al *αβροῖ*) Syr Sah Cop Arm Aeth
- 31 add *ad eum dicens* after *domini* (D) (d) Gig E e
Lat(M W) cor vat, cf Perp (+ *dicens*) = vg⁹⁰
demid Aug Lat(D Θ)
- 32 add *sum* after *ego* d E e Perp vg⁹⁰ cor vat Lat(D Θ S
U W) Arm Bede Gig c demid
- 35 add *super nos* after *iudicem* D d Harcl h. e c demid
Greek (≠ C 81) Perp Gig Lat(C G Θ I R² S* T U W)
- 39 om *suis* after *cordibus* D d Or
- 40 order = *nos praecedant* Gig (*praeceant*) Ir (*antecedant*)
- 43 *in* for *trans* d e Gig Perp Lat(D) tepl Sah, cf Greek (D)
- 51 *restitutis (obstitutis)* for *resistitis* Perp d Gig Aug
Lucif c m w g² lux Lat(A D G Θ I M R T W)
dura for *duri* Aug Ir Hier Gig e* Lucif Fulg Vig g² c
demid lux m vg⁹⁰ Lat(A* B C F Θ I K O R S T U
V W)
add *et* after *sicut* Aug c e demid t w cor vat Lat(Θ O
S U) Boh Sah, cf Greek (D etc.)
- 52 add *sunt* after *persecuti*, cf d [h] e Perp Aug (all om.
it before)

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- 8 2 *eum* for *illum* d e Perp Gig g² t c vg^{so} cor vat^{ms}
Lat(M O)
- 7 *enim* for *autem* d Lat(F)
- 11 om *suis* d Gig
- 13 om *admirabatur* after *stupens d(obstupiscebat)* e Perp
(*stupebat*)
- 14 *eos* for *illos* D d Lat(B F K M R S U V) Perp Gig vg^{so}
(cf all Greek *αὐτούς*)
- 20 *possidere* Aug e t Lat(I O S) Boh, cf Greek
- 37 add *dixit autem Philippus Si credis ex toto corde licet
et respondens ait Credo dei filium esse iesum* after
baptizari Cypr Ir Harcl E e Gig Perp c demid m t w
Lat(A B D Θ O R T U V W) (D d in lacuna) Greek
(2298 and other min)
- 39 *autem* for *enim* Perp vg^{so} Aug c demid Lat(M R S U)
- 9 1 *spirans* for *aspirans* Aug c demid e Gig Perp² t Amb
vg^{so} Lat(C G Θ M O R^o S T U W)
- 5 add *nazarenus* after *iesus* h Perp (e) t c demid Aug Ilil
Amb Lat(Θ M S U) Greek (A C E 8 25 104 467 801
1838) Syr Boh Aeth Petil
add *durum (vanum h) est tibi contra stimulum calcitrare
et tremens ac stupens dixit, domine, quid me vis facere
et dominus ad eum* after *persequeris* Aug h Harcl Gig
Perp c demid t Eth Amb Lucif Lat(B C D F G² K
O R U V W)
- 6 om *sed* h Harcl Perp c demid t vg^{so} Lat(B C F G K
M O R S U V W)
- 16 order = *eum pati pro nomine meo* h Ir Aug Gig Perp
Lat(B F K O R V W)
- 20 *dominum* for *iesum* h Lat(W), (dnm [ihm]) = m Sah
- 22 om. *multo* h e t Gig Perp demid alb cod caraf Lat(B C
D F G Θ I K O R T W)
- 30 add *nocte* after *cesaream* man 1 = Greek (614 431
1518) Harcl E e Perp Syr Sah; tr. before *cesaream*
man. 2 = Gig Lat(C D O)
- 40 add *in nomine domini nostri iesu christi* after *surge*
Harcl Gig Perp m Lat(D O) Sah Amb Cypr

- 10.4 om *tuae* after *elemosynae* d Perp
 28 *set* for *et* Aug Perp c demid t cor vat^m vg^o Lat(C D Θ I M O T W) Ir
 29 *accersisti* for *accersistis* d c Lat(B F U W Θ)
 30 add *ieiunus* before *orans* D d t cor vat* Gig e Bede Greek (A² H L P S s) Sah Syr Chr
 32 add *is cum venerit loquetur tibi* after *mare* D d e Perp Gig t Bede Greek (C E H L P min) vers
 33 tr *tibi* after *praecepta sunt* D d c Gig t and all Greek add *ad nos* after *veniendo* t w Lat(B² D R) cor vat* = D d q Harcl Perp (which add more in different order)
 36 add *suum* after *verbum* d Gig Perp Lat(B² C G² T) m t Sah, cf 614 (αβροῦ)
 48 order = *eos baptizari in nomine (domini* d Perp) Cyp D d Gig Rebapt E e Perp = Greek (H L P 383 614 etc)
 add *apud eos* after *maneret* D d (before *maneret*) Gig (Perp^o) vg^o Lat(B D I K M R T V W) Sah Boh Syr Eth
 11.1 add *et honorificabant deum* after *dei* Harcl (Gig) (Perp) demid Lat(Θ) q w and 7 Paris MSS
 2 om *in* Harcl Perp vg^o Gig Lat(C I K M O R V W)
 4 add *per* before *ordinem* d e Gig Perp¹ (*ex ordinem*)
 15 *cecidit* for *decidit* d c e Gig Aug demid t Lat(B R S^o U W), (ἐπεσεν) D 206 321
 17 add *ne daret illis spiritum sanctum* D d Harcl Aug (*dare*) Perp* (*dare*) Lat(D Θ O R*) q Paris Lat 11533 Syr Bohem
 add *credentibus in dominum iesum christum* Harcl Lat(Θ) Syr D d (*cred in eum*) and Lat(D O) tepl Paris Lat 11533 (*cred in nom 1 c.*)
 25 add *ad* before *tharsum* D and all Greek (es), cf d Perp (*Tharso*), Harcl (*Tarsi*), e (*in tarsum*)
 29 *quis*[] for *quis* = *quisque* Aug Perp Gig c Lat(R)
 12.12 *cognominatur* for *cognominatus est* d e Gig Perp Lat(G)
 25 *cognominatur* for *cognominatus est* d Gig e Lat(W) Greek (A min) (ἐπικαλούμενον) Sah

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- 13 12 *super doctrina* for *super doctrinam* d e Gig Perp Vig
Hier c demid Lat(D G Θ M° U° V W) vg°° Lucif
- 13 add *erant* after *eo* vg°° d (order changed) e Gig Perp c
demid Lat(A C D M O* R T W)
- 28 *in eo* for *in eum* D d Gig c Harcl Lat(M R¹ U¹ W) vg°°
Sah (most Greek MSS om)
- 32 *eam* for *ea* D d c demid e Perp Lat(A° D G M U V W)
- 33 *in primo psalmo* for *in Psalmo secundo*, man 1, marg
= D d Gig codd Bedae Or Hil; cf Just Tert
Cypr Eus
- 34 *suscitavit* for *suscitaverit* Gig d Hil (e), cf D and all
Greek
- 44 *autem* for *vero* after *sequenti* d Gig
- 14 2 add *persecutionem* after *suscitaverunt* D d Greek (383
614), Lat(D R²) Harcl^m E e Gig w
add *dominus autem pacem cito dedit* after *fratres*
D d E e Harcl Lat(Θ D) demid Gig Perp q w Bede
Cass
- 6 add *et commota est omnis multitudo in doctrina eorum*
paulus autem et barnabas commorabantur lustris after
erant D d e h q w tepl Perp² vg° Bede (Cass), cf E
- 10 order = *voce magna* d Lat(W) Gig
- 16 add *in* before *vias* (*in viam* h) h Perp Lat(F G* Θ* K
R S V)
- 22 *regnum* for *in regnum* [h] cor vat* Lat(G W)
- 23 order = *presbyteros per singulas ecclesias* Harcl Greek
(383 614) E e Gig [h] etc.
- 24 *autem* for *que* after *transeuntes* (*regressi* d) D d Boh
- 15.1 *salvi fieri* for *salvari* d c demid e Gig Perp cor vat
Lat(A C D G Θ I M T W)
- 2 add *dicebat autem paulus manere eos ita ut crediderunt*
after *illos* (*eos* d) D d Gig q w tepl Harcl Ephrem
- 5 *crediderunt* for *crediderant* d demid vg°° Lat(D Θ I S
U W)
- 9 add *et* before *fide* = *et ipsos fidei* of d Cypr Ir Rebapt
- 17 *deum* for *Dominum* D d c Lat(Θ) Rebapt
- 19 *deum* for *Dominum* D d c Gig e Ir vg°° Lat(B C F G
K R V W) and Greek

- 23 *per manum* for *per manus* D e Harcl Lat(B I K R S V)
and all Greek
- 29 add *et ea que vobis fieri non vultis alius ne feceritis* after
fornicatione D d Greek (614) Harcl q w² Perp
Lat(D Θ) Syr Sah Eth Cypr Ir
- 34 add *Visum est autem syle remanere ibi solus autem*
iudas abiit after *illos* D d Gig c q w Harcl Lat(D Θ
M R T) vg^{ss} cor vat Greek (C 383 614) (Sah) Cass
Ephr
- 41 add *precipiens custodire precepta apostolorum et seni-*
orum et cum circumisset has nationes after *ecclesias*
Harcl Gig q w (D d) c demid Lat(D O), cf other Lat
MSS Arm Cass
- 16 7 *illos* for *eos* d Gig
- 28 order = *voce magna* D Gig Lucif Greek (α C E H L P
min) vg^{ss} demid Perp e Lat(D B Θ O R V W) Syr
Arm Chr
- 29 add *ad pedes* after *syle* = demid vg^{ss} Lat(B F G^o Θ K
R S U V W), before *paulo* = D d Gig q Perp Lucif
Cass Lat(A C I M O T) Syr
- 31 *in dominum iesum* for *in Domino Iesu* D c e Gig Perp
(Lucif) Lat(B C F Θ^o K O R U V W)
- 40 add *narraverunt quanta fecisset dominus cum eis et* after
visis fratribus D d Lat(D) Paris Lat 11533 Bohem
consolantes for *consolati sunt* et D Gig
- 17 6 add *et dicentes* after *clamantes* D d w Gig Lat(D R)
- 11 add *quemadmodum paulus annuntiaret* after *haberent*
Harcl Gig Lat(D) Greek (383 614) Prisc Ephr
- 15 add *eum* after *perdixerunt* Harcl e c vg^{ss} demid
Lat(A B¹ I K M R V W) Greek (E H I. P s) Sah
Boh Arm Chr
- 17 om. *et* before *in foro* Aug demid Lat(C T)
- 18 *seminator verborum* for *seminiverbius* Aug Gig Perp²
Lat(B F K R S V W)
- 22 *supersticiosos* for *superstitiosiores* c Lat(R S W), *super-*
stitiosos d demid e Gig Perp² Aug cor vat Lat(B F
Θ K M U V)

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- 18 2 *pontium* for *Ponticum* d h (Pon[*ticum*]?) Lat(Θ)
 add *Paulus* after *ad eos* D d (h m Harcl Syr also other
 changes)
 add *et salutavit eos* Gig q Lat(D Paris Lat MSS) (h
 Lat(R²) order changed)
- 3 *erant* for *erat*² Aug Perp e demid m Or vg^{so} Lat(A¹ C
 D K U V)
- 4 add *et disputabat in sinagoga per omne sabbatum
 interponens nomen domini iesu* after *scenofactoriae
 artis* (D d h) c demid e q w (Gig Harcl) Lat(D Θ W)
 cor vat* Bede vg^{so}
- 6 add *sua* after *vestimenta* D d h Gig vg^{so} demid c
 Lat(D Θ M K S) Greek min Syr Sah Boh
 add *paulus* before *dixit* D d h w Lat(C T W)
- 13 *credere* for *colere* h Lat(W)
- 21 add *oportet me solempnem diem facere ierosolimis et
 after dicens (dixit d)* D d Greek (H L P S 383 614)
 Gig demid Lat(D Θ M* W) q w
- 24 *genere* for *natione* Aug e cor vat^{ms} Lat(W) vg^{so}
- 26 *domini* for *Dei* Aug Perp E e c demid vg^{so} Lat(C D G^o
 Θ R W) Greek min
- 27 *crediderunt* for *crediderant* Aug Gig Perp Lat(B D F K
 S T U W)
- 19.5 add *christi* after *iesu* D d [pap^{ss}] Gig Syr Sah Hier Petil
 Lat(Θ W) sang^{1ss} Greek (383 421 614)
- 6 *eis* for *illis* d Lat(R T)
- 9 add *ab hora quinta usque in horam decimam* after
tyranni D d Harcl Greek (383 614) Gig w Ambrst
 Lat(D G^o Θ)
- 23 add *domini* after *de via* d Harcl Perp Gig c demid
 Lat(B C D F G^o K O R S T U V W) vg^{so} Cass Syr
 Arm
- 26 add *et* after *set* D Gig Greek (A L min) demid Syr Chr²
 Thphyl
- 33 *autem* for *ergo* D d e c Gig vg^{so} Lat(W) and most
 Greek

- 38 *proconsules* for *pro consulibus* d Gig Perp³ c e demid
Lat(A¹ B D G^o K M R V W)
add *se* after *accusent* d cor vat* Lat(W)
- 20 1 *convocatis* for *vocatis* d (*convocavit*) e Gig Lat(I O W),
cf Greek Syr Arm Eth
- 13 *vero* for *autem* d Gig
- *21 *per dominum* for *in dominum* D
- 24 add *verbi* after *ministerium* D d Gig demid cor vat^{ms}
vg^{so} Amb Lucif Ephr Lat(Θ M)
- 33 *et* for *aut*¹ D m c Perp Aug demid cor vat^{ms} Lat(B C
G^o Θ K M R S T U V W)
- 21 1 add *deinde in hyram*, cf *καὶ μὴρα* D Sah cor vat*
Lat(Θ) Gig Paris Lat(7 202 11505*)
- 2 add *in* before *phenicem* D and all Greek, vg^{so} E e demid
Lat(B F G I K R S U V W)
- 22.7 add *durum est tibi contra stimulum calcitrare* after
persequeris Harcl E e Gig Lat(D) demid Ath Bede
Syr
- *17 order = *mihi revertenti* e, cf d = Greek
- 26 add *ei* after *nuntiavit* D Harcl vg^{so} Gig(illi) demid
Lat(S U) Greek (99)
- *23 10 *ab eis paulus* for *Paulus ab ipsis* h (c)
- 13 add *vir* after *XL* Harcl vg^{so} c Lat(B K R V W)
- 19 *eius* for *illius* h e s Gig
- 20 order = *perducas paulum* h c Gig Greek (L 614 1518)
- 25 add *timuit enim ne forte raperent eum iudaei et occiderent*
et ipse postea calumpniam sustineret quasi pecuniam
accepturus after *presidem* Harcl Gig cor vat* Perp
Lat(D M R) w Cass vg^{so} Greek (614 2147) (D lacuna)
- 35 om *et* Harcl vg^{so} c Gig Perp Lat(B C D F K R S T U
V W) Greek (614 2138 2147) Syr Boh Thphyl
- 24 7 add *voluimus secundum legem nostram iudicare super-*
veniens autem tribunus lysias cum vi magna eripuit
eum de manibus nostris iubens accusatores eius venire
ad te after *apprehensum* for *adprehendimus* Harcl^{60x}
Gig Perp³ c demid Greek (ψ 614) E e Syr Cass Bede
Lat(A¹ B D I K M R V W) vg^{so}

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- 25 23 om. *et* before *iubente* Harcl Gig Perp c demid s vg^{ss}
Lat(B C F G^e I K M R S T U V W) Greek min
- 27 2 *incipientes* for *incipientem* h Gig demid vg^{ss} Lat(F I M
S T V W) cor vat^{ms} Greek (H L P etc.)
- 4 *cyprum* for *Cypro* Gig Perp* h s vg^{ss} Lat(B F S U
V W) demid
- 5 add *xv diebus* after *navigantes* h Lat(D) Harcl Greek
(614 2147 min)
- *6 order = *navem centurio* h (*navem Alexandrinam cen-
turio*)
- 28 16 add *ipsi foris extra castra* after *sibimet* Harcl Greek
(614 1611 2147) Gig Perp demid cor vat Lat(Θ* W)
q w and 7 MSS Paris Lat
- 29 add *et cum hec dixisset egressi sunt iudei multam inter
se habentes questionem* after *audient* Harcl c Perp
Gig vg^{ss} Cass Greek (383 614 etc) Lat(C D Θ M
T W)
- 30 add *iudeos atque grecos* after *ad eum* Harcl Lat(C R T
W) (Gig) (Perp) Greek (614 1245 1518 1611 1765
2005)

The agreements of the pure Western sources with MS 146
are tabulated as follows

TABLE IV

Sources	Additions	Word usage	Word-order	Syntax	Omissions	Totals
Aug	9	13	3	9	2	36
Cypr	5	1	3	0	0	9
D	6	3	0	4	0	13
d	9	20	3	13	5	50
D and d	31	13	7	5	4	60
Harcl	33	1	3	2	4	43
h	9	8	9	2	4	32
Ir	4	5	4	3	3	19

Table IV shows that Codex Bezae (d) in the Latin (which
follows the Greek text of D¹ very closely) gives most support
to our manuscript. Counting all cases of D d there is support

¹ Jackson-Lake, *op cit*, p lxxxiii (D is the oldest Greek text of the Acts with
Western readings and it is the only one that offers any continuity)

in 123 out of the total (181) supported variants. The Harclean Syriac is next in frequency of support, with Augustine, the Fleury Palimpsest and Cyprian's text, and Irenaeus following. The support is distributed among all five types of variants in all the sources except Cyprian, which contains only a small portion of the text of Acts. Only 57 of these variants are supported by the Sixtine and Clementine editions of the Vulgate, and only 77 by Lat(W), which stands nearest of all Vulgate manuscripts.

The fact that the greatest support in most of the sources is in the additions bears out the usually accepted view that the additions are characteristic of the *Western* text, and, in this, allies our manuscript with the *Western* influence. These additions have been observed especially in the African form¹ of the Old-Latin, and this for MS 146 is sustained through the support shown by Cyprian and h in 9 and 32 variants, 5 and 9 of which respectively are additions. In the case of 2 variants h is the sole support.

The support of Augustine and Irenaeus also tends to confirm the evidence of relationship to an African tradition in these variants. The Latin translation of Irenaeus' work was probably made between A.D. 370 and 420 in North Africa² and Augustine's text of the Acts was like the Cyprianic text of A.D. 280 used in the church of Hippo.³ In one variant Augustine is the sole support.

The Harclean Syriac gives support in 43 variants, 33 of which are additions. This version with the apparatus of Thomas of Harkel is one of the most important witnesses to the *Western* text of the Acts.⁴

In the support given by the *Western* sources there are only

¹ P. Corsen, *Der cyprianische Text der Acta Apostolorum*, Berlin, 1892, Burkitt, *Texts and Studies*, iv, 3, p. 46 ff.

² *Old-Latin Biblical Texts*, vii, pp. 15-18, lxx-lxi.

³ Jackson-Lake, *op. cit.*, p. cxv.

⁴ Jackson-Lake, *op. cit.*, p. clxi, *ibid.*, p. ccviii for the statement that D and the Harclean Syriac apparatus probably go back to a common *Western* original, but the two lines show types of mixture of different character and independent of one another.

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7 instances¹ of sole support by individual manuscripts. These are distributed as follows: order (3), word-usage (2) and syntax (2). The sources that give this sole support are d (1), D (1), h (3), e (1) and Aug (1).

MS 146 AND THE EUROPEAN TEXT OF THE ACTS

MS 146 is supported in the following variants by the Old-Latin versions related to the Gigas recension, or the so-called *European* text, including the Spanish Old-Latin

- 1 4 add *inquit* after *audistis* Perp^m Aug D c demid etc²
- 6 *convenerant* for *convenerunt* Perp Gig c t demid vg^{so}
Lat(B C F G^o Θ^o K M R S T U W)
- 15 om *et* d Perp^{*} vg^{so} etc
- 17 *qui* for *quia* Perp Gig d Aug etc
- 20 *eius* for *eorum* Perp Gig(*illius*) Aug Ir = D and all
Greek
inhabitet for *habitet* e Gig c d etc
add *alter* before *alius* (a conflate), *alter* = Perp Gig e t
Aug Ir vg^{so} Lat(A D Θ V W) lux cor vat
- 2 1 add *discipuli* after *omnes* Perp² cor vat Auct de prom
Lat(U W)
- 4 *varius* for *alius* Perp c t Aug Vict etc
- 8 *linguam nostram* for *lingua nostra* Perp² vg^{so} demid c
etc
- 9 om *et* after *Mesopotamiam* Perp Gig D d c Aug Tert
vg^{so} etc
- 13 *irridebant dicentes* for *inridentes dicebant* Gig (Clark,
not W and W.) D d Aug Syr
- 14 *elevavit* for *levavit* Perp c d t Aug etc.
- 18 om *super*² Gig Lat(B C F K M R W) Pass Perpet
Prisc Hier Tert
- 23 *affligentes* for *adfigentes* Perp² vg^{so} Lat(D W) demid
cor vat

¹ See the notations with the asterisk in the list of *Western* support, *supra*, pp 12-22

² In case the text variants are cited in full in the previous list, only important authorities are cited here

- 26 *requiescit* for *requiescet* Perp* arg lux Lat(A F G Θ* I O S V)
- 28 transpose *mihī* after *notas* Perp c lux Lat(A C D M S T U V W)
- 29 om. *et* after *quoniam* Perp d Ir Gig c etc
- 32 *nos omnes* for *omnes nos* Gig Perp c d Ir etc
- 36 *igitur* foi *ergo* e Vict, cf *itaque* Gig Perp Tert
- 38 add *domini* after *nomine* E c Lucif D d Cypr Perp
(*dnī nrī*) etc
order = *spiritus sancti* Perp Gig c t demid Cypr etc
- 40 *verbis plurimis* for *verbis pluribus* Perp e Aug etc
- 41 order = *in die illa* e Harcl etc
- 3 3 add *ab eis* (man 2) after *elemosinam* E e Perp² q
Lat(Θ S) Cop Syr, cf D d h Perp¹ etc
- 7 order = *manu eius* Lucif Perp (*manum eius*) h Cypr
Gig etc
- 11 *cucurrit* for *concurrit* Perp² c demid vg^{ss} Lat(W)
- 12 *potestate* for *pietate* Perp² h Lat(W) etc
- 18 *qui* for *quae* Gig Vig c demid vg^{ss} Lat(O R V^{ss} W)
- 19 order = *peccata vestra* Perp Gig D d h m Ir Tert vg^{ss}
etc
- 25 *nostros* for *vestros* Perp Gig D d h Ir etc
om *et*² Gig Perp c demid Lat(C D F G Θ^o R T U^o)
- 4 3 *eos* for *eis* Lucif Gig Perp(*illos*) c demid Lat(D Θ M U)
- *4 *eorum* for *virorum* Gig and early editions
- 8 add *audite* after *seniores* Perp² Gig Cypr Greek (E 94
307 327 al) vg^{ss} Lat(Θ W) c Bede Syr Aeth
- 21 add *in eo quod acciderat* after *fuera*t (for *erat*) Perp²
(Lucif) Bede vg^{ss} c demid cod mult Lat
- 30 *sanctum* for *sancti* Perp Arm, cf Bede, retract 118
in Graeco habetur per nomen sancti pueri tui iesu
- 32 add *unum* after *cor* Perp Gig Harcl etc
- 5 7 *eius* for *ipsius* d Perp Gig Lucif c etc
- 8 add *mulier* after *mihī* Perp² demid vg^{ss} Lat(B F K R S
U V W)
- 9 add *dixit* after *autem* e Gig (*inquit*) Perp (*et dixit*)
Greek (A E P S 383 462 etc) Harcl Sah

- 10 *eam* for *illam* e Gig d
- *12 om. *autem* after *manus* Lucif, cf d (*vero*) B (re) Syr Eth
- 15 *plateis* for *plateas* Perp² Lucif Gig e etc
add *et liberarentur ab infirmitatibus suis* Gig (Perp) Lucif E e vg^{so} etc.
- 16 om *et* after *autem* Lucif D d Gig Lat(D S T)
- 21 *in templo* for *in templum* Perp Gig e
- *26 add *templi* after *magistratus* Perp; cf E e (ἐν τῷ ἱερῷ) q
- 29 order = *oportet obedire* Gig Lucif (D om *oportet*)
- 36 order = *numerus virorum* Gig Perp D d h Greek (383 614) etc
- *40 add *amplius* after *ne* Perp, cf Lat(C T)
- 6 I *factum* for *factus* Gig c demid Lat(A C F¹ I O T W) vg^{so}
- 3 add *santo* after *spiritu* e c t h demid etc
- 4 order = *erimus instantes* Harcl Gig (*adservientes*), cf Dst t
- 7 *domini* for *Dei* E e Perp c t etc.
- 8 order = *signa et prodigia* E e Gig Perp g² Syr Gaud Cass
- 13 *dicentes* for *qui dicerent* c e Gig Perp etc
order = *falsos testes* Gig g² vg^{so} Lat(I M)
- 15 add *in* before *eum* e Gig Perp etc.
- 7 2 *moretetur* for *moraretur* Perp² m² Gig d (*mortuus esset*)
- 4 add *et inde transmigravit illum in terra caldeorum* after *in charram* Perp² m² Lat(Θ) but before *et dixit* of 7.3
- 5 *set* for *et*² c Gig vg^{so} etc
- 6 add *ei* before *deus* Gig c demid etc
- 7 *deservient* for *servient* Gig Perp e etc.
dicit dominus for *dixit Deus* Perp d Ir Gig etc
- 8 add *genuit* after *Isaac*² E e Perp Syr Boh Lat(O)
- 11 *super* for *in* D d E e etc
- 14 add *suam* after *cognationem* E e Gig Perp Lat(C T W) vg^{so}, cf D d (*eius*) Greek min Syr Sah Cop Aeth
- 17 *quod* for *quam* e Gig Lat(W)
- 19 add *nostros* after *patres* E e Gig Perp c vg^{so} demid Lat(A¹ B C D G K M R S T U V W) Greek (A C 383 614 etc)

- 22 om *in* before *operibus* Perp Gig e d etc
 24 add *de genere suo* after *iniuriam* E Gig d etc
 25 add *suos* after *fratres* Perp e etc
 26 *in pace* for *in pacem* Perp Gig c demid cor vat^{ms} vg^{so}
 Lat(D G Θ I M T U V W)
 27 add *suo* after *proximo* Gig q w Lat(A D K S U V W^o)
 29 order = *duos filios* Perp Lat(D)
 31 add *ad eum dicens* after *domini* Gig (Perp) E e etc
 32 add *sum* after *ego* Gig Perp E e Bede vg^{so} etc
 35 add *super nos* after *iudicem* E e Gig Perp (*iudicem aut*
 principem super nos) c d t demid etc
 39 add *eum* after *reppulerunt* Perp² Gig demid q cor vat*
 Lat(C D G^o T)
 *42 order = *XL annis* Gig
 43 *in* for *trans* Gig Perp e d etc
 44 add *cum* before *patribus* Perp² demid cor vat* Lat(A¹ S)
 vg^{so}, cf D* d E etc
 add *deus* before *loquens* Perp² Lat(D R²) w demid vg^{so}
 cor vat*
 48 *per prophetam* for *propheta* Gig vg^{so} Lat(W), cf Lat(M)
 49 om *est*² Perp* Gig = B and all Greek except D etc
 **requiescionis* for *requietionis* Perp, cf Lat(S)
 51 *dura* for *duri* Gig e* g² c demid lux m Or Lucif Aug etc
 restitutis for *resistitis* Perp Lucif Gig (*obstitutis*) etc
 add *et* after *sicut* e c demid Aug etc
 52 add *sunt* after *persecuti* Perp d [h] e (all om before)
 56 order = *stantem a dextris* Perp Gig vg^{so} Tert Lat(F
 G V)
 60 add *in domino* after *obdormiuit* Perp q w Lat(B K
 V W) vg^{so}
 8 2 *eum* for *illum* Perp d Gig e etc
 *5 add *iesum* after *christum* Gig (om *christum*)
 6 *intendebat* for *intendebant* Perp* Lat(I)
 7 *exibant* for *exiebant* Gig c demid vg^{so} Lat(W)
 *9 om. *esse* Gig, cf. d (om *se*)
 11 om *suus* Gig d
 13 om *admirabatur* e Perp d

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- 14 *eos* for *illos* Perp Gig d etc
 18 *illis* for *eis* Perp Gig
 20 *possidere* for *possideri* e t Aug etc
 *24 *eorum* for *horum* Perp
 25 *redibant* for *rediebant* Gig c vg^{so} Lat(W)
 33 *tolletur* for *tollitur* Perp e c t demid vg^{so} Lat(A C D Θ I O R T U W) Ir
 36 *quis* for *quid* Perp Gig t Lat(F G^o V)
 37 add *dixit autem philippus Si credis ex toto corde licet et respondens ait credo dei filium esse iesum* after *baptizari* E e Perp Gig c t m etc
 39 *autem* for *enim* Perp c demid vg^{so} etc
 91 *spirans* for *aspirans* Perp^a Gig e c demid t Amb Aug etc
 2 om *in* before *ierusalem* Perp c Lat(B F G K R V W)
 5 add *nazarenus* after *iesus* E Perp h c demid etc
 add *durum est tibi contra stimulum calcitrare et tremens ac stupens dixit Domine, quid me vis facere et dominus ad eum* after *persequeris* Perp Gig c t w demid Lucif etc
 6 om. *sed* Perp c t vg^{so} etc
 11 *surgens* for *surge* Gig e c demid t alb arg cor vat Lat(A B C D G^{*} I^{*} K R^{*} T U^{*} V^{*} W) Greek
 16 order = *eum pati pro nomine meo* Gig Perp h etc
 17 order = *dominus iesus misit me* Perp Lat(A K U V W) Syr Boh
 22 om *multo* Gig Perp e t h etc.
invallescebat for *convalescebat* Perp^{*} e Lat(W), cf. Greek
 26 *quod* for *quia* Perp e cor vat^{ms} vg^{so} Lat(W)
 27 add *domini* before *iesu* Perp Greek (056^{*} 35 104 383 1522^o etc); cf *iesu christi* Lat(Θ)
 30 add *nocte* after *cesaream* Perp Gig w E e etc
 31 order = *spiritus sancti* Perp Gig demid Lat(D Θ) Boh Sah
 32 *transiret* for *pertransiret* e Perp (*transeuntem*) cor vat Lat(B K R S V W)

- 34 *enea* for *Aeneas* e Perp Gig c vg^{so} Lat(B C Θ^o K M R T V W) Greek Boh Sah
 sanet for *sanat* Perp c w Amb vg^a Lat(B K R¹ S U W)
 add *dominus* before *iesus* Gig Perp c t Lat(A B² Θ I M O T W) vg^{so} Greek (A etc) Sah Amb Cass
- 39 *eum* for *illum*² Gig demid m Lat(O), cf *ei* Perp e Greek
- 40 add *in nomine domini nostri iesu christi* after *Tabita*
 surge Gig Perp Cypr m etc
- 10 4 add *in* before *eum* Gig Perp demid Lat(A B² C O T U*), cf *els aβρόν* 98 915 1311
 quis es for *quid est* Perp c vg^{so} Lat(G^o I R T W) Greek (1828) (vacat D)
 om *tuae* after *elemosynae* Perp d
- 6 add *hic dicit tibi quid te oporteat facere* after *mare*
 Perp² Greek (466 467) Eth vg^{so} Lat(D)
- 10 *illis* for *eis* Perp Gig c cor vat^{ms} Lat(W) vg^{so} Chr
 Greek (L P 31 383 614 min)
- 25 add *venit* before *Cornelius* Lat(M T) Bede Perp²
 (before *ei*) = vg^{so} Lat(C G² W) c, cf (D d Gig)
- 28 *set* for *et* Perp c t (Ir) vg^{so} demid etc
- 30 add *ieiunus* before *orans* Gig e t Bede etc
- 32 add *Is cum venerit (qui adveniens* Perp) *loquetur tibi*
 after *mare* l'erp* Gig e t Bede etc
- 33 transpose *tibi* after *praecepta sunt* Gig c t etc
 add *ad nos* after *veniendo* (Perp d) t w etc
- 34 add *suum* after *os* E e Perp c demid t vg^{so} Lat(B G² Θ K M R² S U W) Greek (κ^o A C 383 etc)
- 36 add *suum* after *verbum* Perp Gig d m t etc
- 48 order = *eos baptizari in nomine* E e Perp (+ domini)
 Gig etc
 add *apud eos* before *aliquot* Gig (*illos*) Perp (*se*) vg^{so} etc
- 11 1 add *et honorificabant (magnificabant* Perp²) *deum* after
 dei Gig Perp² q w Harcl etc.
- 2 om *in* Perp Gig vg^{so} Harcl etc
- 4 add *per* before *ordinem* Gig Perp¹ (*ex*) d e
- 15 *cecidit* for *decidit* Gig c e demid etc
- 17 add *ne daret illis spiritum sanctum* after *dominum*
 Perp Aug etc.

- *19 order = *que fuerat facta* Perp³ (*fuit*) (om. *facta* Perp*)
Lat(R^{ms})
- 23 order = *permanere proposito cordis sui in domino* Perp
Gig (om *sui*)
- 25 add *ad* before *tharsum* (els *Tapov*) E e (in) D and all
Greek
- 29 *quis*[] = *quisque* for *quis* Perp Gig c Aug Lat(R)
- 12 3 *ut apprehenderet* for *adprehendere* Gig Lucif (*compre-*
henderet) vg^{so} cor vat Lat(B K W)
- 4 *custodiendum* for *custodire eum* Lucif Gig Perp vg^{so} c
demid Lat(B R* W)
- 8 *caligas* for *galliculas* Gig Bede vg^{so} Lat(B Θ K M R T
U V W)
- 12 *cognominatur* for *cognominatus est* Gig Perp e d
Lat(G)
- 25 *cognominatur* for *cognominatus est* Gig e d etc
- 13 2 add *illis* before *spiritus* E (e) c demid vg^{so} Lat(Θ W
etc) Vig
- segregate michi* for *separate michi* Perp Gig c demid m
Lucif vg^{so} Lat(A K M O V W)
- quo* for *quod* Perp³ c m sang¹³³ Vig Lat(Θ° O R W)
- 3 *eos* for *illos* Perp Gig e Lucif Ambr Vig Lat(Θ)
- 5 *salamnam* Perp³ vg^{so} c
- 6 *virum magnum* for *virum magum* Perp* (*n* of *magnum*
exp Perp³) Lat(B D G* K S T* U* V), Gig Lucif
om *magum*
- barieu* for *Bariesu* Perp³ c demid Lat(G° M S° U W) vg^{so}
- 7 *Saulo* for *Paulo*³ Perp demid vg^{so} Lat(G O U) = *Saulum*
vg^{so} D d e Gig Lucif Bede
- 12 *super doctrina* for *super doctrinam* Gig Perp e Lucif c
etc
- 13 add *erant* Perp Gig e c demid etc
- 20 *samuelem* for *Samuhel* Perp³ Lat(C Θ O R)
- 21 om *deus* Gig Lat(D G O R* S W) Greek min[†]
- 28 *in eo* for *in eum* Gig D d c vg^{so} Harcl etc
- 32 *eam* for *ea* Perp e c demid etc.
- 33 *in primo psalmo* man. 1 marg Gig Hil D d etc.

- 34 *suscitavit* for *suscitaverit* Gig d e (*resuscitavit*) Hil etc.
- 44 *autem* for *vero* Gig d
dei for *Domini* e demid cor vat vg^{so} Lat(W) Greek
 (B* C E L P etc.)
- 46 *iudicatis* for *iudicastis* c e demid cor vat vg^{so} Lat(Θ* K
 S T V W)
- 14 2 add *persecutionem* after *suscitaverunt* E e Gig w D etc.
 add *dominus (deus) autem pacem cito dedit* after *fratres*
 E e (om *cito*) D d Harcl demid Gig Perp etc
- 6 add *et commota est omnis multitudo in doctrina eorum*
paulus autem et barnabas commorabantur listris after
erant E e D d h Perp² q w etc
- 10 order = *voce magna* Gig d Lat(W)
- 16 add *in* before *vias* Perp h e (*per*) etc
- 23 order = *presbyteros per singulas ecclesias* E e [h] Gig
 Harcl Greek (383 614 H L P s) Sah Chr
- 15.1 *salvi fieri* for *salvari* Perp Gig e c demid etc
- 2 add *dicebat autem paulus manere eos ita ut crediderunt*
 after *illos* Gig D d q w etc.
- 3 *conversationem* for *conversionem* e Lat(A B D F* I K M
 R S* U V W)
pertransibant Perp^o c vg^{so} Lat(C W)
- 19 *deum* for *Dominum* Gig e c vg^{so} etc
- 29 add *et ea quae vobis fieri non vultis alius ne feceritis* after
fornicatione Perp d q w² etc
sanguine suffocato Perp* cor vat Lat(A B F Θ I K R*
 S* V W) Greek (Σ^o A² etc.)
- *32 add *eos* after *confirmaverunt* Gig, cf Lat(O)
- 34 add *visum est autem syle remanere ibi solus autem iudas*
abijt after *illos* Gig D d c q w etc
- 39 add *quidem* after *Barnabas* Gig c vg^{so} Lat(B C F K S
 T U V W)
- 40 *dei* for *Domini* E e Gig vg^{so} Lat(B W) Greek (C H L
 P s)
- 41 add *praecipiens custodire praecepta apostolorum et*
seniorum et cum circumisset has nationes after
ecclesias Gig c demid q w etc
ecclesiam for *ecclesias* Perp Lat(W)

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- 16 2 add *bonum* after *testimonium* G1g Perp² cor vat* vg^{so}
Lat(B C F K¹ S T U W)
- 6 order = *spiritu sancto* G1g c demid vg^{so} Lat(A B D I
M W) V1g Hier
- 7 add *in* before *Bithiniam* e G1g vg^{so} Lat(O W)
illos for *eos* G1g d
- 10 *quod* for *quia* e vg^{so} Lat(B F K R S U V W)
- 12 *prima pars* for *prima partis* E Perp² demid Sah
- 17 *nobis* for *vobis* e Lat(R) Greek (A C² H L P 383 614
etc) Eth Sah Or
- 22 add *eos* after *iusserunt* G1g Lucif Perp c demid vg^{so}
Lat(A¹ B K O R S U V W) Sah Syr
- 28 order = *voce magna* G1g Lucif Perp e demid etc
- 29 add *ad pedes* after *syle* G1g demid Perp Lucif etc
(order changed)
- 31 *dominum iesum* for *Domino Iesu* G1g Perp (Lucif) e c
etc
- 40 *consolantes* for *consolati sunt . . . et* G1g D
- 17 3 order = *iesus christus* E e vg^{so} cor vat* Lat(B D O W)
Greek (x 383 434 614 1108 1245 1611 1765 1838 2005)
Boh Syr Arm
- 4 *gentilibus et* for *gentilibusque* Perp e, Lat(C W), which
om *que*, cf G1g *et de grecis*
- 6 add *et dicentes* after *clamantes* G1g D d w etc
- 7 add *nescio quem* after *dicentes* G1g (after *esse*) Paris
Lat 11533* (before *dicentes*)
- 9 *accepta satisfactione* for *accepto satis* Lat(K M^o U¹ W)
Perp² demid vg^{so}
- 10 *venissent* for *venisset* e cor vat^{ms} vg^{so} Lat(B K O R*
S V)
- 11 add *quemadmodum paulus annuntiaret* after *haberent*
G1g Harcl Lat(D) etc.
- 13 *Beroe* for *Beroeae* Perp Lat(Θ^o I R W) (A C Θ* M
O U)
- 15 add *eum* after *perduxerunt* e c demid Lat(A B¹ I K M
R V W) vg^{so} etc.

- 18 add *dicebant* after *alii vero* Gig Perp² c demid cor vat
Lat(C D R T V^o W)
seminator verborum for *seminiverbius* Gig Perp² Aug
etc
- 22 *supersticiosos* for *superstitiosiores* Gig Perp² e c demid
etc.
- *32 order = *cum autem audissent* Perp
- 18 2 add *et salutavit eos* after *ad eos* Gig h w etc.
- 3 order = *artis erat* e Gig Lat(C)
erant for *erat*² Perp e demid m Aug etc
- 4 add *et disputabat in sinagoga per omne sabbatum inter-*
ponens nomen domini iesu after *scenofactoriae* e c
demid Gig (D d h) vg^{so} q w etc
- 5 order = *iesum christum* Gig Lat(F T) Greek (209 383
614) Syr
- 6 add *sua* after *vestimenta* Gig c demid vg^{so} etc.
- 15 om *et*² Perp c vg^a Lat(C D* T U^o W), cf *vel* h
- 21 add *oportet me solempnem diem facere ierosolymis et*
after *dicens* Gig demid q w etc
- 24 *genere* for *natione* e cor vat Lat(W) vg^{so} Aug
- 26 *domini* for *Dei* E e Perp c demid Aug etc
- 27 *crediderunt* for *crediderant* Gig Perp Aug etc
- 19 2 add *dixerunt* after *illi* Gig Perp c demid vg^{so} Lat(B D
G² I K M O R S U V W) Greek (H L P S etc.) Syr
Boh Sah
- 4 *baptismo* for *baptisma* Perp² c demid cor vat vg^{so}
Lat(M W) Sah Eth
- 5 add *christi* after *iesu* Gig d [pap^{so}] etc
- 9 add *domini* after *viam* E e Gig c demid lux vg^{so}
Lat(A¹ C D Θ K M R T V W) Syr
add *ab hora quinta usque in horam decimam* after
tyranni Gig D d w etc
- 19 *eis* for *his* e vg^{so} Lat(B K R V W)
- 23 om. *in* Perp cor vat* vg^{so} Lat(B C Θ I K O R S T U
V W)
add *domini* after *de via* Gig d Harcl Perp c demid etc
- 26 add *et* after *set* Gig D demid etc.
order = *turbam multam* Perp Lat(D I)

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- 33 *autem* for *ergo* Gig c d e etc.
 38 *proconsules* for *pro consulibus* Gig Perp² e c d demid etc.
 20.1 *convocatis* for *vocatis* Gig e Lat(I O W) d etc.
 4 *sosipater* for *Sopater* Gig Perp² c demid vg^a Lat(D G^a M R S U W) Bede
 5 *sustinuerunt* for *sustinebant* Gig c vg^{so} Lat(B F I K R S U V W)
 7 *venissemus* for *convenissemus* Gig Perp^a Lat(O W)
 add *cum* before *eis* Perp vg^{so}
 9 add *oblatus* after *sublatus* Perp² cor vat^a Lat(B K V W); cf cor vat^{ms} Lat(R²)
 11 *in* for *ad* Perp e c demid cor vat^{ms} vg^{so} Lat(B C F G K R T V W)
 13 *vero* for *autem* Gig d
 14 *invenisset* for *convenisset* Perp² Lat(B K S^a V)
 24 add *verbi* after *ministerium* Gig D d Lucif vg^{so} demid etc.
 26 add *vestrum* after *omnium* E e Lat(U) Bohem Greek min Syr
 33 *et* for *aut*¹ Perp c demid D etc
 21.1 add *deinde in hiram* after *patharam* Gig (*myram*) Paris Lat(7 202 11505^a) etc.
 2 add *in* before *phenicem* E e demid D etc
 3 *apparuissemus* for *paruissemus* Perp² e c demid vg^{so} Lat(B D K R V W)
 om *et*¹ Gig c demid vg^{so} Lat(R T U^a W) Greek (A etc)
 5 *expletis* for *explicitis* Gig Perp c demid vg^{so} Lat(B D F G^a Θ I K M O R S U V W), cf D vg Sah
 11 order = *iudei in ierusalem* Gig demid Lat(Θ) Amb Syr
 16 *iasonem* for *mnasonem* Gig Perp demid vg^a Lat(D G 1 O R S^a U W) x Boh
 *20 *et* for *at* Perp
 26 *eis* for *illis* e Lat(W); *ipsis* d
 27 *de* for *ab* e c demid cor vat vg^{so} Lat(B C F Θ K O S T U V W)
 *28 om. *populum* Gig (om. *populum et*)

- 22 2 *loqueretur* for *loquitur* Perp² c vg^{so} Lat(B K R U¹ V W);
cf Greek (L min) Lat(D) e
- 3 *gamalielis* for *gamaliel* Perp c cor vat^{ms}, cf. Greek
(B etc)
- 7 add *durum est tibi contra stimulum calcitrare* after
persequeris E e Gig Harcl demid etc.
- 16 add *et* before *baptizare* Perp² c vg^{so} Lat(B F G^o Θ I K
R S U V W)
- 21 *ad* for *in* Gig Vig Ambrst Lat(B F K R S U W)
- 22 *huiusmodi* for *eiusmodi* Perp vg^{so} Lat(D M O W)
- 26 add *ei* after *nuntiavit* Gig (*illi*) demid D etc
- 27 add *si* after *mihi* Perp² c demid vg^{so} Lat(B G Θ K R
V W) Greek (L P etc)
- 23 6 add *de* before *resurrectione* e Tert Lat(A C D M T)
- *10 om *de medio eorum ac deducere eum* Lucif, cf. 8
- 11 add *in* before *ierusalem* Lucif e vg^{so} Lat(B C D G^o K
O R S T U V W)
- 14 *ad principem* for *ad principes* Gig Perp
- 19 *eius* for *illius* Gig e s h
- 21 add *quam* after *amplius* Perp² c demid vg^{so} Lat(B D K
O M R U V W)
- 23 *convocatis* for *vocatis* Gig c Lat(B K U V W), cf. Greek
- 25 add *timuit enim ne forte raperent eum iudaei et occiderent*
et ipse postea calumpniam sustineret quasi pecuniam
accepturus after *praesidem* Gig Perp² Harcl w etc
- 26 add *ei* after *scribens* Perp cor vat Lat(B F K S² U V)
vg^{so}
- 30 add *eum* after *misit* Gig demid cor vat* Lat(C M R S
T U W) Eth
- 32 *in* for *ad* e Lat(O W) Greek
- 35 om. *et* Gig Perp c vg^{so} Harcl etc
- 24.1 *audierunt* for *adierunt* Perp* Lat(C T)
- 3 *suscepimus* for *suscipimus* Gig Perp c Lat(B C G^o Θ
I K O R S U V W)
- 7 add *voluimus secundum legem nostram iudicare super-*
veniens autem tribunus lysias cum vi magna eripuit

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- eum de manibus nostris iubens accusatores eius venire ad te* after *apprehensum* for *adprehendimus* Gig Perp² E e c demid Harcl etc.
- 19 add *et apprehenderunt me clamantes et dicentes Tolle inimicum nostrum* after *tumultu* Perp² c demid Eth Lat(D Θ) cor vat* vg*, cf Gig (21, 36)
- 25 order = *post autem aliquot* E e and Greek MSS
- 25 3 add *in* before *ierusalem* e c vg^{so} Lat(C D F Θ M R T)
- 4 add *quidem* before *paulum* c Lat(C M T), after *Paulum* Gig Lucif
- 7 add *ei* after *obicientes* Perp Lat(I S U) Greek (L etc.) Syr Boh Arm
- 8 *lege* for *legem* Perp Lucif Lat(F R S W)
- 13 and 23 *beronice* for *bernice* Gig e demid Lat(G^o T) (Θ C) Greek (C)
- 22 add *dixit* after *autem* Perp c vg^{so} Lat(B K R V W)
- 23 om *et* before *iubente* Perp Gig s c demid Harcl etc
- 24 om *hic* Perp e c demid vg^{so} Lat(C G^o M R T) w
- 27 *causam* for *causas* Gig Lat(B D I K O R S T W) Syr Arm Eth
- 26 17 *populis* for *populo* Perp² c vg^s Lat(A B C K M R T V W)
- 19 *celesti visioni* for *caelestis visionis* Gig Perp c demid vg^{so} Lat(R² W), cf Lat(D)
- 25 *et* for *at* Perp c demid Lat(B D K M R S U V) vg^{so}
- 29 om. *hos* Gig vg^{so} Lat(W) Greek
- 27 2 *incipientes* for *incipientem* Gig h demid c s etc
- 4 *cyprum* for *Cypro* s Gig Perp* c demid vg^{so} h etc
- 7 *iuxta* for *secundum* Perp² c demid Lat(D^{ms} F K R S U V)
- 11 *nauclo* for *nauclo* Perp c vg^{so} Lat(I M R S^o T U W)
- 28 add *bolidem* after *submittentes* Gig Perp² s c demid cor vat vg^{so} Lat(C D Θ T V^{so})
- 40 *sustulissent* for *abstulissent* Perp² vg^{so} Lat(B K R S U V)

- 28.1 *mitilene* for *Militene* Perp³ c Lat(T)
vocabatur for *vocatur* Perp c demid vg⁹⁰ Lat(D Θ I K
M R T V)
- *10 add *nobis* before *imposuerunt* Gig
- 11 *castrorum* for *Castorum* Perp c Lat(A* B D F G* Θ I
K O R S* T* U* W)
- 16 add *ipsi* (cf Lat(C T) *apud semed ipsum*) *foris extra*
castra after *sibimet* Gig Perp cor vat⁹⁰ Harcl q w
demid etc
- 18 order = *mortis esset* Perp Gig s Boh Lat(D O R*)
Greek
- 27 *eos* for *illos* Gig Perp demid vg⁹⁰ Hier
- 29 add *et cum hec dixisset egressi sunt (exierunt Perp)*
iudei multam (multo Perp¹ multas Perp²) inter se
habentes questionem (quaestiones Perp²) after *et ipsi*
audient Gig Perp vg⁹⁰ c Harcl etc
- 30 add *disputans* after *conducto* (Lat C T W) and *iudeus et*
grecos after *ad eum* q Ephr Harcl Lat(C R T W)
= *et disputabat cum iudeis et grecis* after *ad eum*
Gig Perp
- 31 om *amen* Gig Perp* c vg⁹⁰ Lat(B C D G I K M O S T
U V W) Greek

TABLE V
CLASSIFIED AGREEMENTS WITH MS 146

Sources	Additions	Word-usage	Word-order	Syntax	Omissions	Totals
E e	20	5	5	0	0	30
E	5	2	0	2	1	10
e	14	26	4	19	3	66
Gig	66	44	24	37	17	188
Lucif	9	4	3	9	3	28
Perp	66	61	19	43	16	205
s	1	1	1	2	1	6
c	56	58	15	50	16	195
demid	48	42	5	32	8	135

Table V shows the support given by the *European* text to MS 146. There are in all 320 variants, of which 109 find support in vg⁹⁰, 113 variants are supported only by members

of the European family Perp¹ gives most support, 205 variants. The agreement between Perp and our manuscript is distributed among all five types of variants with the largest number found in additions (66).

There are 50 instances where Perp² has been corrected to readings that agree with MS 146 as opposed to Vulgate readings 22 of these are additions, 16 are word-usage, 11 are grammatical, and 1 is word-order

It is interesting to note that of the 66 additions supported in Perp many are single words or phrases, though there is also support for the long additions that were found in the *Western* text support Of the total support in Perp there are 7 variants, apart from spelling, for which it offers the sole support for our manuscript These are distributed respectively: additions (2), word-usage (2), word-order (2), syntax (1), and no omissions

After Perp Codex Gigas is next in frequency of support, including 188 variants, for 7 of which it is the sole support. Though Gig is a thirteenth-century manuscript, the text in the Acts represents a Latin text current in the fourth century³

E and e either singly or together support MS 146 in 106 variants of which 39 are additions These are often in agreement with Vulgate manuscripts as A, and with Gig and Perp, in fact e⁴ is sometimes regarded as the precursor of Gig and is known to have been in England in the eighth century, whence perhaps its relation to the text of A⁵

Lucifer gives support 28 times, distributed among all the types of variants In 2 omissions it is the sole support. The fragment s⁶ is in agreement in 6 variants, evenly dis-

¹ For a discussion of the Perpignan MS and the Old-Latin in it, cf S Berger, *Notices et extraits des manuscrits de la bibliothèque nationale*, 35, Part 1, pp 169 ff

² Corrections in Perp are from the Languedocian type of text in which Western readings were valued Cf Jackson-Lake, *op cit*, p cviii, also p ccxx, S Berger, *Histoire de la Vulgate* (Le texte languedocien), p 72 et seq

³ Jackson-Lake, *op cit*, p cx for the statement that this is known from the agreement with quotations in Lucifer of Cagliari, who wrote A.D. 355-362

⁴ Cf Jackson-Lake, *op cit*, p cxi

⁵ Jackson-Lake, *op cit*, p lxxv

⁶ *Old-Latin Biblical Texts*, IV, p xviii for a discussion of the close relationship of s and Gig

tributed over the five types. Both these text sources cover but little of the text of Acts. The Old Latin MSS c and demid are less pure types of the European text, but give much support. Of the 113 variants supported only by the European sources, there are 30 additions, 37 word-usage, 25 grammatical, 11 omissions, and 10 word-order.

Perp appears to offer the greatest support and represents almost all known types of Old-Latin.¹ It issued from south-west France and shows more particularly Spanish influence.² In Spain,³ as in Ireland, the African Old-Latin was the early text that later came into rivalry with the Vulgate.

This relationship of the European text to our manuscript may be conjectured to be due partly to an agreement among the European, Old-African, and Old-Irish traditions. Because of the fragmentary condition of our Old-African sources and the fact that the Old-Irish text in the Acts has not been established, we can not positively determine the extent of this hypothetical agreement. We do know, however, that the Bible reached Ireland before the time of the Vulgate.⁴ Hence the first text must have been related to the Old-African. It probably came by way of England, though the relationship to the Perpignan manuscript, as well as to Spanish manuscripts of the Vulgate, points towards Spain.

Another explanation for part of this agreement might be that manuscripts executed in Ireland in the fifth and sixth centuries, which were subsequently sent to France as well as to Italy and Switzerland, influenced the local Biblical traditions.⁵ Furthermore, as we have seen above in the discussion of Table II, some of the agreements with the European text may have come into the tradition of MS 146 along with the revision to the Vulgate.

¹ Jülicher, *op cit*, pp 180-182

² Berger, *op cit*, 35, Part I, pp 183-188

³ Jackson-Lake, *op cit*, p cxxxii

⁴ Berger, *Histoire de la Vulgate*, p 46 et seq for "Les Irlandais en Europe", also Hoskier, *Concerning the Genesis of the Versions of the New Testament*, I, p 13

⁵ Berger, *loc cit*.

TABLE VI

TOTALS

Variants Supported by	Additions	Word-usage	Word-order	Syntax	Omissions	Totals
Western Text	68	49	20	27	17	181
European Text	110	87	34	62	27	320
Both Texts	57	34	17	23	13	144

Table VI presents a summary of Tables IV and V which shows the Old-Latin support of MS 146 in variant readings from the Vulgate. There is also the additional tabulation of the variants (included above in the computation of the Western and European text-support) in which both types of text are in agreement with MS 146. By subtraction we find that the Western text supports MS 146 in 37 variants without the European, while the European text has 176 cases of support without the Western.

Because of the larger number and greater completeness of the representatives of the European text, this is probably not a fair comparison, but nevertheless we may be sure that MS 146 is more closely related to the European text. Yet 37 of its important Western variants are found in no representative of the European text. Therefore that text is not the sole source, and perhaps not even the chief source for its Old-Latin readings.

VARIANTS WITH MISCELLANEOUS SUPPORT OR UNSUPPORTED

Additions in MS 146 form the greatest number of variants from the Vulgate readings. There are 206, of which 68 are supported in the *Western* Old-Latin sources, and 110 in the *European* Old-Latin, with an agreement between the two texts in 57 additions. There remain some that represent readings of miscellaneous Greek or Latin sources, often in paraphrase, or are unsupported. These additions most frequently are in the form of a qualifying word or word-group. Others are conjunctive particles, prepositions, words used as subjects, objects (direct and indirect), and verbs. There are

ten obvious errors due to conflation or dittography as in 4.19, 5.42, 10 29, 13.35, 19 14, 20 7, 20 9, 24 26, 26 26, or to other possible palaeographical confusion as in 10 28. Seven corrections by first or second hand restore the text to the Vulgate form, cf 1.19, 4 31, 5 26, 13.44, 20 7, 24 26, 26 3. The 36 additions without other manuscript support are marked sol. All additions not discussed above are included in this list. Some are, and more may be, from an Irish Old-Latin text.

- 1 19 add *a* before *lingua* man 1 sol
- 3 18 add *suorum* after *prophetarum* cor vat* Vig
- 25 add *autem* after *vos* sol
- 4 19 add *ad eos* before *dixerunt* Greek (383 614 etc.) (Gig om.), a conflate of Vulgate with older text.
- 31 add *sunt* after *omnes* man 1 sol
- 32 add *ex his* after *eorum* sol, a conflate
- 33 add *nostris* after *domini* vg^{ss} Lat(Θ) Greek (36* 94 307)
- *5 21 add *ministros* after *miserunt* Lat(D)
- 34 add *vir* after *honorabilis* cor vat Lat(W)
- *40 add *eis* after *denunciaverunt* Lat(W), cf. *eos* e Gig Lucif, cf d (*eis praeceperunt*) Lat(C T)
- 42 add *domos* after *domos* sol
- 6.7 add *erat* after *discipulorum* sol, cf erasure of 4 letters Lat(I)
- 13 add *blasphemie* after *verba* lux Greek (383 614 etc.) t c Lat(S U) Arm Cass Aeth Chr (from vers 11)
- *7 42 add *se* after *convertit autem* Paris Lat 11533, cf h (*pervertit illos*) Greek (C) Sah Lat(G) (*eos*)
- *43 add *propter hoc* before *in* (for *trans*) Lat(W)
- 44 add *illis* after *disposuit* cor vat* vg^{ss}
- 55 add *stephanus* before *plenus* Greek (614) q m cor vat* Lat(G^o M S U W)
- 60 add *quia nesciunt quid faciunt* after *hoc peccatum* cor vat* Lat(W)
- 8 6 add *verba* before *audientes* sol, cf Greek αὐτοῖς
- 9 9 add *ibi* after *erat* vg^{ss}
- 20 add *ingressus paulus* after *continuo* alb Lat(B K R V) m, cf vg^{ss} c cor vat^{ms} Lat(W) (om *paulus*)

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- 29 add *gentibus* after *autem* (for *quoque*) c vg^{ss} Lat(B F R S U V W), cf. Lat(D O) *cum gentibus*
- 31 add *et* before *ecclesia* sol ; cf. ἡ μὲν οὖν ἐκκλησία κ A B C
- 40 add *sua* after *genua* Lat(G² Θ T)
- 42 add *iesu christo* after *domino* sol , cf. t (+ *nostrum iesum christum*)
- 43 add *per* before *dies multos* sol.
- 10 9 add *domus* before *in superiora* = cor vat^{ms} Lat(B²), which add after
- 13 add *dicens* after *eum* w Lat(B²)
- 28 *dixit itaque* for *dixitque* sol , cf. *aitque* d; *dixit* t Lat(I)
- 29 add *ego* after *ergo* sol , cf. Lat(T) *ego* for *ergo*
- 36 add *dominus* after *misit* sol , cf. *deus* cor vat^{*} demid vg^{ss} Lat(W)
- 46 add *illo* after *loquentes* sol
- 11 5 add *vas* after *vas quoddam* sol , cf. transposition in Greek (181 1898)
- 12 12 add *petrus* before *marcus* sol
- 16 add *ostium* after *aperuissent* vg^a c cor vat^{*} Lat(B K R U V)
- 13.35 *alibi ait dicit* for *alias dicit* sol , *alibi* = t cor vat^{ms} Lat(W)
- 36 add *in* before *sua* c demid vg^{ss} Lat(C K R V W)
- 44 add *die* before *sabbatho* man. 1 sol.
- *14 4 add *illius* before *civitatis* Lat(G^o)
- *15 31 add *gaudio magno* after *gavisi sunt* Lat(G)
- 33 add *aliquanto* before *tempore* vg^{ss} Lat(D O), cf. Lat(G I M R) c demid cor vat
- 16 21 add *nobis* after *annuntiant* sol.
- 31 add *ei* after *dixerunt* Lat(O) Sah Syr Eth
- 17.12 add *multitudo* before *gentilium* sol.
- 18 13 add *in* before *deum* sol , cf. *credere* for *colere* h Lat(W)
- 14 add *suum* after *os* sol , cf. *eius* Lat(O)
- 19 5 add *et cum* after *his* man. 2 sol , cf. d *cum audissent*
- 14 add *quidam* after *quidam* sol.
- 33 add *quendam* before *alexandrum* cor vat^{*} Lat(D)

- 20 7 add *protexit* before *protraxitque* sol., cf. Lat(U)
protaxitque
- 9 add *oblatus* (after *sublatus*) sol, a conflate reading;
sublatus from Vulgate
- 11 add *est* after *allocutus* cor vat vg* Lat(Θ V W)
add *et* before *sic* vg* cor vat* Lat(V W); cf *sicque*
Lat(S U)
- *19 add *et mansuetudine* after *humilitate* cor vat*
- 21.8 add *unus* before *de septem* vg^{so} c demid sang 133
Lat(B D F G^o K R S U V W)
- 16 add *secum* after *adducentes* vg^{so} c Lat(C M R^a T)
- *28 add *nos* after *adiuvate* Lat(D)
- 23 8 add *sanctum* before *spiritum* man 2 sol
- 24 add *eum* after *paulum* c Lat(B F K R S W)
- *25 add *verba* before *haec* Lat(W), cf *hunc mundum*
Lat(D), *formam hanc* c Gig Greek
- 34 add *esset* after *cilitia* cor vat* Lat(S U), *ἐστίν*, *κ*
A 441 etc
- 24 20 add *modo* before *apud te* cor vat* Lat(C T)
- 25 add *dominum* before *iesum* sol
- 26 add *enim* before *autem* (del man 1) sol, a conflate
from Greek
- 25.16 add *quae ei obiciuntur* after *crimina* cor vat* w Lat(D)
- 22 add *respondens festus* after *audire* sol, cf Lat(Θ S U);
cf Syr demid (om *ait*) *et festus ait*
- 26.21 add *volentes me* after *temptabant* Lat(B K R S U V W)
- 26 add *enim* after *enim¹* sol, dittography, cf 2 47 in d
autem autem
- 28 add *inquit* after *modico* sol, cf *ait* before *in* h e
Lat(C T), *dixit* Gig
- 29 add *ait* after *opto* sol, cf h (*ad quem sic ait*) (om.
Paulus) Greek (H L P etc)
- *27 4 add *nos* after *sustulissemus* Lat(G^o)
- 12 add *apium*, before *portum* sol, cf + *apud* Perp³
- *20 add *neque luna* after *autem* Lat(D)
- 21 add *me* after *quidem* sol, cf *vos* Gig s
- 25 add *meo* after *deo* c demid Lat(B F K R S U V W)

- 27 add *die* after *decima* cor vat* Lat(V W)
 28 add *et* after *qui* vg** Lat(B K R S U V W); a conflate,
 cf Lat(I) Gig Greek *et* for *qui*
 37 add *numero* before *ducente LXX* sex sol.
 43 add *in mare* after *se* c demid vg* Lat(A B K R V)
 28 15 add *appu* after *fratres* Lat(V) Paris Lat (2, 4*)
 18 add *alia* after *nulla* sol
 26 add *ad eos* after *dix* c demid vg** Lat(B F K R S U V)

Among the 60 omissions not supported in the recognized sources of the Western or European text are some that agree with miscellaneous Greek or Latin sources. There are 17 cases of the correction of such omissions by first or second hand to the Vulgate form (2 11, 2.21, 2.47, 3 10, 3 17, 3 23, 5.36; 8 21, 8 33, 14 23, 15 2, 18 26, 19 4; 21 18; 21.28, 21 38, 22 14). These are so numerous that they seem to have come from comparison with a Vulgate manuscript, or more likely from corrections in the margin or between the lines of the parent manuscript. Such additions are more easily overlooked than words standing in the original text. There are 35 unsupported omissions in MS 146

- 1 7 om *dixit autem eis* sol, cf. *et dixit* D Gig Perp tol, om.
 eis Aug^{ab}
 2 5 om *iudaer* Lat(O) ✕
 11 om *nostris* man 1; sol, cf. transposition Gig Lat(D);
 suis Aug
 *13 om *autem* Lat(D), cf. d (*vero*)
 21 om *erit*, man 1, t Lat(Θ I M O T)
 25 om *est* after *dextris meis* sol.
 *47 om *autem* after *dominus* t* (+ t²); cf. *autem autem* of d
 om. *cottidie* man 1, sol, cf. d *cottie*
 *3 2 om *in* before *templum* Lat(A) *templo*
 10 om *templi* man. 1, sol.
 17 om *per ignorantiam* man 1, sol
 20 *cum venerint* c demid vers angl 1611 against *ut cum*
 venerint of most MSS
 21 om *est* after *locutus* sol.
 23 om *non* man 1, sol.

- 4.13 om *et* between *constantiam* and *Iohannis* man. 1 sol.
 24 om *et* before *mare* c demid vg^{ss} Lat(M O R T U) Boh
 36 om *genere* after *cyprius* sol , cf *e* (*natione*)
 5 38 om *et* before *nunc* Lat(C T) , cf *h* *autem* for *et*
 6 12 om *et* before *scribas* sol , cf Gig g² ac
 7 29 om *moses* before *in verbo isto* sol , cf Lat(D), *mōy* for
Mouses
 30 om *et* before *expletis annis* Lat(Θ M W)
 32 om *autem* Lat(A) Boh (3 MSS), cf *d* (-*que*)
 8.11 om *magis suis* sol , cf om *suis* d Gig
 21 om *tibi* man 1, sol , cf Lat(W) transpose *pars tibi*
 9 1 om. *autem* before *adhuc* Lat(W) Greek (κ^c B² A C) , cf
 Greek (κ^{*} 104 319 322 450 605) Sah (om *adhuc*)
 22 om *autem* sol , cf *vero* Perp
 24 om *autem* after *custodiebant* sol , cf. Gig Perp Lat(G
 I^{*} S) om *et* and Greek (H P S min) Syr Aeth Chr *τε*
 for *δε* *κα*
 25 om. *per murum* before *dimiserunt* sol , cf transposition
 in Gig Greek (H L P 383 614)
 37 om *autem* Lat(D F G Θ R) Greek (81)
 13 11 om *Domini* sol
 34 om. *iam* before *non t* Lat(W) Hil, cf *d* Gig Greek
 min om. *amplius*
 14 23 om *cum* before *constituissent* man 1 sol , cf *h* (*et*
constituerunt)
 15.2 om. *non minima* after *seditione* man 1 sol ; cf *d* (*facta*
seditione et quaestione non modica) = all Greek ex-
 cept E
 39 om *autem* after *facta est* sol , cf. *ὅτι* Greek (C E H L
 P min) Syr Arm Chr and *et* Gig Perp
 16.9 om. *per noctem* after *visio* sol
 24 om. *in* before *ligno* vg^{ss} Lat(B F K S V W)
 17 13 om. *et* after *venerunt* sol
 24 om *in* before *manufactis* Lat(Θ W)
 18 11 om. *autem* after *sedit* sol , cf *et* D d h Greek (E H L P
 etc) *τε*
 26 om. *coepit* man 1, sol., add after *hic* man 1, sol.

- 20 7 om *in* before *una* vg^{ss} Lat(B C F K S T U V W)
 *11 *satis* for *satsique* Lat(R)
- 21 8 om *in* c sang 133 vg^{ss} Lat(B F K R S U V W)
 18 om *nobiscum* man. 1, sol., cf. Gig Syr *intravimus cum Paulo*
- 23 om. *tibi* after *quod* Lat(B K S V W)
 *37 om *cum* before *cepisset* Lat(S*)
- 38 om *in desertum* after *eduxisti* man 1 sol, cf *deserto* Gig
- 22 3 om *legis* after *aemulator* Greek 614 Chr 1/3 Lat(C I T W), cf. *τοῦ θεοῦ* of Greek and other versions exc. Harcl
- 14 om *ex ore* man 1, sol.
 22 om. *cum* after *autem* Greek min (1518) Lat(B F K R V W)
 om *suam* after *vocem* sol, transpose Greek (33 69 431 623 1838)
- 23 9 om. *autem* sol
 20 om *te* after *rogare* sol
- 25 7 om *cum* after *Qui* sol
 8 om *autem* after *Paulo* cor vat^{ms} vg^{ss} Lat(D W), cf. Greek (383 etc) Chr (*ἀπολογούμενου αὐτοῦ*)
- 19 om *vero* before *quasdam* sol
- 26 22 om *sunt* before *locuti* sol, cf transposition e s vg^{ss} Lat(C T)
- 27 31 om *hi* after *nisi* Lat(C I* V), cf *isti* s
- 28 15 om *Appii* before *forum* Lat(V) Paris Lat(2 4*); see above section on additions
- 27 om *enim* sol, cf Perp* *autem*

Spelling, which, as a type, forms the largest portion of variants from the Vulgate readings, has not been included in the tabulations. There is little support of these variants in the individual Vulgate manuscripts. In the ~~SC~~ editions there is more agreement. The *Western* sources give considerable support, in some of which d is the only one to agree.¹ Noteworthy is the support that D gives MS 146 in the con-

¹ Clark, *The Acts of the Apostles*, p. lxxv

sistent employment of \overline{IHC} and \overline{XPC} as abbreviations for *Iesus* and *Christus*. Because of their appearance in Latin manuscripts they have been described as Latinized forms of the normal \overline{IC} and \overline{XC} in Greek manuscripts, but they occur in all the older Greek papyri and in the Sahidic and Bohairic versions. The evidence seems to indicate that \overline{IHC} and \overline{XPC} were prior to \overline{IC} and \overline{XC} and were transliterated into Latin at an early date. The most support in spelling is found in the European sources, especially in Gig and Perp. In some cases either one or both of these furnish sole support. The greater variant-support in spellings found in the European sources does not necessarily prove important in determining relationship. The agreements with Perp and Gig may indicate the spellings that prevailed at the period in which the manuscripts were written. Our manuscript does not agree with Perp in its Spanish or Languedocian peculiarities of spelling and this fact would tend to show that some of the agreements noted are characteristic of twelfth and thirteenth century manuscripts.

In a study of the orthographical variations certain characteristics appear dominant

- 1 The assimilation of the preposition in composition
- 2 The interchange of vowels or consonants *o* for *u*, *p* for *b*,
t for *d*, *ch* for *h*, *n* for *m* before *q*, *t* for *c*
- 3 *e* for *ae* and *oe*
4. The omission of the initial aspirate
5. The addition of an aspirate between vowels and after *t*.
There is vacillation in this usage.
- 6 The addition of *p* between *m* and *n* and after *m* before *t*.
7. Greek *v* becomes *i* or *y*
Greek *i* becomes *y*, also Greek *η*
- 8 The omission of *e* in fourth conjugation verbs (Imperfect Indicative).
- 9 *ii* for *i*.
10. The consonant *c* or *t* doubled between vowels.
11. The retention of *s* after *ex* in composition. Variation is found in this usage.

Proper names that form a part of the spelling variants with weak support or none follow

- 2 9 *capadoceam* for *Cappadociam* sol.
aryam for *Asiam* sol.
- 4 6 *cayphas* for *Cataphas* Gig Lat(I)
- 5 3 *sathanas* for *Satanas* Gig Lat(C R W)
- 6 5 *procorum* for *Prochorum* Lat(B D G Θ K M R T U
V W)
thimonem for *Timonem* Lat(C I M R¹ W)
**anthiochenum* for *Antiochenum* Lat(R)
- 7 16 *sichen* for *Sychem* sol
- 43 *babilonem* for *Babylonem* Lat(G R T W)
- *8 28 *ysayam* for *Esaiam* Gig
- 9 36 *thabitha* for *Tabita* sol
- 13 8 *elimas* for *Elymas* Lat(B D K M O* S T U V W) Gig
- 14 *psidie* for *Pisidiae* cor vat* Lat(K M*)
- 14 11 *licaonie* for *Lycaonice* sol ; cf Lat(C) *lycaoniae*
- 19 *yconio* for *Iconio* Gig c Lat(I U*)
- 21 *yconium* for *Iconium* Gig c Lat(C I)
- *15 40 *syla* for *Sila* Lat(I)
- *16 1 *thimotheus* for *Timotheus* Lat(C)
- 6 *phrygiam* for *Phrygiam* Lat(R V W)
- 7 *mysiam* for *Mysiam* Lat(Θ M* O S U* W)
bithyniam for *Bithyniam* Lat(D G Θ R W)
- 11 *trohade* for *Troade* sol
- 14 *liddia* for *Lydia* Lat(O R S T U W) (16 40 *liddiam*,
9 32 *lidde*)
**thiatirenorum* for *Thyatirenorum* Lat(Θ*)
- 16 *phitonem* for *Pythonem* Perp c Lat(R¹ U W)
- *17 1 *amphibolim* for *Amphipolim* Lat(R)
**thesalonicam* for *Thessalonicam* Lat(M)
- 19 29 *aristarco* for *Aristarcho* (20 4 *aristharcus*) Lat(G M S
T U)
- 20.4 *pirri* for *Pyrri* Gig Perp c Lat(R T W)
- 9 *euthicus* for *Eutychus* Lat(B D Θ I M R) Gig Perp
- 14 *mytilenaem* for *Mytilenen*, cf vg^o d *mytilenen*
- 21.1 *patharam* for *Patara* sol
chorum for *Cho* sol , cf. *choum* Gig Perp etc.

- 7 *ptolomaidam* for *Ptolomaida* cor vat^{ms} Lat(A U)
 22 3 *cilitie* for *Ciliciae* Lat(B K U)
 27 2 *hadrimetinam* for *Hadrumetinam* sol
 thessolonicense for *Thessalonicense* sol , cf Lat(D)
 *5 *cylicie* for *Ciliciae* Lat(D)
 8 *thesalia* (man 1) for *Thalassa* sol., cf Lat(W) *thessala*
 12 *affricum* for *Africum* Lat(O W)

In the syntactical variants our manuscript finds support in from 17 to 32 variants in the individual Vulgate manuscripts compared, there are 67 agreements with the ~~MC~~ editions, 27 with *Western* sources, and 62 with European sources as already shown. An error due to palaeographical confusion of abbreviations occurs in 13 2 (*quo* for *quod*); in 28 15 there is perhaps a confusion between the accusative and ablative cases (*tribus tabernas* man 1 for *Tribus Tabernis*), see above, p 12. There are 10 corrections to the Vulgate form 1 19, 2 26, 5 15, 9 2, 10 5, 15 41, 16 4, 16 23, 20 24, 18 15. The list follows of those variants that are supported in miscellaneous sources or are unsupported. There are 23 of the latter

- 1 9 *hoc* for *haec* sol
 2 31 *videre* for *vidit* sol
 3 26 *suscitatis* for *suscitans* sol
 4.2 *quid* for *quod* sol
 8 *princeps* for *principes* man 1 (corr man 3) sol
 22 *fuera*t for *erat*² c vg^{so} Lat(A R)
 25 *in spiritu sancto* for *spiritu sancto* sol , cf *per* Cop
 Greek and d h Gig etc
 5 5 *audierunt* for *audierant* cor vat vg^{so} Lat(D), cf. d Gig
 Lucif
 22 *venerunt* for *venissent* sol
 42 *cessabunt* for *cessabant* sol
 7 6 *semen tuum* for *semen eius* = σοῦ Greek (x 94 307 322)
 Sah Cop Syr Aeth vg^a
 24 *quandam* for *quendam* sol
 33 *calciamenta* for *calciamentum* c Lat(C O S T U) Bede
 40 *moysi huic* for *Moses hic* c Lat(Θ I) vg^a cor vat

- 43 *eos* for *eas* sol.; cf. *d eis*
 51 *incircumcisis* for *incircumcisi* vg^{ss} Lat(B F G* K R V W)
 8 4 *pertransibant* c demid vg^{ss} Lat(B C R S T U V W)
 33 *generationes* for *generationem* sol
 10 5 *cognominabat* (man. 1) for *cognominatur* (man. 2) sol
 *22 *accersiri* for *accersire* Lat(W)
 *28 *coniungere* for *coniungi* Lat(W), cf. *adherere* d Gig
 *39 *regionem* for *regione* Lat(Θ*)
 11 29 *in ministerio* for *in ministerium* Lat(O R S*)
 13 11 *circuiens* vg^{ss} Lat(A M)
 13 *navigasset* for *navigassent* Lat(B Θ K M R* U V W)
 27 *habitant* for *habitabant* c demid t Lat(C D O R W)
 14 1 *iconi* for *in Iconio* vg^{ss} Lat(B F G* S W)
 15 8 *illi* for *illis* demid Lat(B I)
 16 3 *erat* for *esset* vg^{ss} Lat(W)
 4 *pertransissent* for *pertransirent* man 1 Lat(C G* R) (Θ*)
 *23 *custodirent* for *custodiret* man. 1 Lat(F)
 17 29 *cum sumus* for *cum simus* Lat(D F O)
 18.18 *totonderat* for *totonderant* vg^{ss} Lat(D F* G K O R U V W), cf. h Greek Boh Sah Syr Eth
 19 *habeant* for *habebant* sol
 19 1 *de discipulis* for *discipulos* vg* Lat(W)
 13 *adiuramus* for *adiuro* Lat(D), *ὀρκίζομεν* Greek (H L P S and min) or *ἐξορκίζομεν* Pap^{ss} 36* 94 307 322 424* 429* 431 450 712 1302 etc. 383 614 Syr
 20.4 *asyam* for *Asiani* sol., cf. Harcl *ex Asia Ephesi*
 21 16 *Cesareano* for *Caesarea* sol.
 29 *introduxis* for *introduxisset* sol
 32 *decurrit* for *decucurrit* demid vg^{ss} Lat(D M S*)
 22 16 *abluer* for *ablue* Lat(B K S V W)
 17 *in templum* for *in templo* sol
 25 *astrinxisset* for *adstrinxissent* Lat(W) Greek (H S etc)
 *23 9 *exurgens* for *surgentes* Lat(W)
 19 *manus* for *manum* sol.
 30 *paraverant* for *paraverunt* vg^{ss} Lat (many MSS including T, not A D F O)

- 24 14 *deo patri* for *patrio deo* cor vat Lat(T W), cf. vg^{ss}
 17 *in gentes meas* for *in gentem meam* cor vat^{ms} Lat(W)
 20 *accusarent* for *accusare* Lat(B F G K S T U* V)
 21 *invenerint* for *invenerunt* sol
 24 *custodire* for *custodiri* vg^{ss} and all Lat MSS exc G*
 Θ* I*
 25 21 *servare* for *servari* sol
 27 1 *tradiderat* for *tradi* sol ; cf Greek *παρεδίδουν* and h s
 demid Harcl (*tradidit*)
 34 *nullus* for *nullius* sol
 *39 *facta* for *factus* Lat(D)
 28 1 *vocabatur* for *vocatur* vg^{ss}
 15 *tabernas* for *tabernis* c demid vg^{ss} Lat(D), which all
 have *tres tabernas*
 22 *rogavimus* for *rogamus* sol
 23 *eis* for *eos* c vg^{ss} Lat(B C F K M R S T U V W)

MS 146 shows in word-usage more variation from the Vulgate than in any other type of reading except the additions and spelling. In these we find support in the individual Vulgate manuscripts for from 18 up to 40 variants, in the *Western* sources 49 agreements, in the *European* sources 87, and 58 in the *SC* editions.

There are 13 corrections by first or second hand to the Vulgate form 1 20, 3 11, 7 8, 9 27, 11 28, 12 19, 16 19, 23 19, 23 32, 25 16, 27 21, 27 33, 28 6. The following scribal errors, mostly by the scribe of MS 146, are detected among these variants after a comparison with the Greek

- 4 10 *votum sit* for *notum sit* (γνωσθὲν ἔστω) sol
 7 38 *sollicitudine* for *solitudine* (ἐρήμω) sol
 *11 9 *mandavit* for *mundavit* (ἐκαθάρισεν) Lat(D)
 28 *famam* for *famem* (λιμὸν) Lat(M¹ B)
 *17.21 *discere* for *dicere* (λέγειν) Lat(D)
 18.11 *dicens* for *docens* (διδάσκων) sol
 21 14 *sudere* from *suadere* (πειθομένου αὐτοῦ) sol.
 24 1 *aratore* for *oratore* (ῥήτορος τινος) sol.
 27.21 *anchora* for *a Creta* (ἀπὸ τῆς κρήτης) sol
 Another possible error may be seen in 23.20.

The list of variants (word-usage) follows which in several instances find some support in Latin or Greek usage. 35 are singular readings of this type in MS 146

- 2 34 *ille* for *ipse* (αὐτός) sol
 3 2 *homo* for *vir* (ἄνθρωπος) sol
 20 *nobis* for *vobis* Tert res carn 23
 23 *quae* man 1 for *quaecumque* c demid vg^{ss} Lat(A G Θ M), *que* (D I)
quaeque man 2, sol, a conflate from Lat(D I)
 4 9 *diudicamur* for *iudicamur* c demid Amb cor vat vg^{ss}
 Lat(A C G Θ I M O R² T U¹ W)
 18 *nec* for *neque* (μηδέ) sol.
 30 *in eo quo* for *in eo cum* sol., cf *in eo quod* vg^{ss} Perp c e demid etc
 5 23 *custodias* for *custodes* sol
 *7 32 *vestrorum* for *tuorum* Lat(W)
 9 5 *at* for *et* Lat(T U); cf *δέ* of Greek, *vero* of Perp
 17 *illi* for *ei* sol
ut for *et* before *implearis* sol.
 23 *concilium* for *consilium* cor vat* Lat(W)
 29 *autem* for *quoque* sol.
 10 2 *familia* for *domo* (οἶκος) sol.
dominum for *Deum*² Lat(G S U W)
 18 *invocassent* for *vocassent* sol, cf ἐπικαλούμενος
 30 *ad* for *in* before *hanc* vg^{ss} Lat(B F K O R¹ S U V W)
coram for *ante* sol, cf d e Perp *in conspectu meo*
 38 *transit* for *pertransiuit* sol
 *11.2 *adisset* for *ascendisset* cor vat (D πορευθῆναι, d *pro-*
ficisci)
 17 *dominum* for *Deum* sol (*deum* in ras Lat B)
 *23 *domini* for *Dei* Lat(W)
 12 7 *excitavit* for *suscitavit* c demid vg^{ss} Lat(B F K V W)
 13 *videndum* for *audiendum* c vg^{ss} Lat(B F K S U V W)
 19 *in iudea* for *a Iudaea* (man 1) sol
 *14 22 *regnum celorum* for *in regnum Dei* Lat(W)
 15.2 *aluis* for *illis* c demid vg^{ss} Lat(A B D G Θ I K M R S*
 U V W)

- *9 *decrevit* for *discrevit* Lat(D)
 *38 *ut quia* for *qui* Lat(R), cf *ut qui* c vg^{ss} Lat(B F G^s K V W)
- *16 19 *spiritus* for *spes* man i, Lat(D)
 26 *ergo* for *vero* sol, cf *autem* d e Gig
 33 *omnis domus* for *omnes* c demid tepl vg^{ss} Lat(A B C G^s I K M^{*} R T U V W)
- 17 14 *cum* for *tunc* sol., om D d Harcl Greek (383 614) Sah
 34 *herentes* for *adhaerentes* sol, cf Greek κολληθέντες
- 18 14 *fascinus* for *facinus* sol
 19.6 *cum autem* for *et cum* sol
 10 *dei* for *Domini* sol
 25 *eiusmodi* for *huiusmodi* c cor vat^{*} Lat(B G Θ I K O R S U V)
- 20.9 *ductus* for *eductus* c demid vg^{ss} Lat(B F K R S U^{*} V W)
- *11 *accedens* for *ascendens* Lat(W)
gustansque for *et gustans* sol
- 21 40 *et manu silentio facto* for *et magno silentio facto* sol
- *22 28 *civitatem* for *civitem* Bede
 29 *ligasset* for *alligasset* Lat(B F K V W), cf. δεδεκώς
- 23 15 *consilio* for *concilio* Lat(B D F G Θ K O S U W)
adducat for *producat* Lat(B K R^s S V W), cf. *deducat* e Gig Lucif
- 16 *introivit* for *intravit* sol
 18 *ostendere* for *loqui* sol; cf. h G₁g (*quod tibi inducet*)
- *20 *perducas* for *producas* Lat(D)
- *21 *illum* for *eum* Lat(W)
- 24.2 *accito* for *citato* c Lat(R), cf Lat(D) *tacito*
 3 *hec* for *et*, cf. G₁g om *et*
utique for *ubique* Lat(B K)
- 6 *quia* for *qui* sol
 16 *consciam* for *conscientiam* sol
 26 *tremefactus* for *timefactus* c demid vg^{ss} Lat(D Θ^{*} I M O R T)
- *28 *porticum* for *Porcium* Lat(B^{*}), *Portium* vg^{ss}, *ponticum*, *Perp^s*

- 25 14 *ibidem morarentur* for *ibi demorarentur* c Lat(B C Θ I K R T V W)
 16 *donec* for *priusquam*, man 1, sol
 24 *vobiscum* for *nobiscum* sol
 26 6 *subnectus* for *subiectus* sol
 7 *servientes* for *deservientes* Lat(B F K S T V W)
 8 *qui* for *quid* sol.
 20 *per* for *in* before *omnem regionem* sol, om Greek (x A B 383) tol
 31 *qui cum* for *et cum* Lat(B F I K R S U V)
 27 10 *vestrarum* for *nostrarum* sol
 32 *abscidere* for *excidere* c Lat(D), cf Lat(U)
 34 *sumere* for *accipere* sol., cf μεταλαβεῖν and προσλαβεῖν
 28 4 *in manu* for *de manu* Lat(B F K R S U V)
 *6 *in timorem* for *in tumorem* man. 1 Lat(D)
expectantibus for *sperantibus* demid cor vat^{ms} vg^{ss}, cf. Greek
 11 *vero* for *autem* sol

MS 146 has more unsupported variants (50) in word-order than in any other type of variant reading. Of the total 128 variants of this type 20 are supported in the Old-Latin of the *Western* sources, 34 in the *European* Old-Latin, and 34 in the *BE* editions. There is some support in the individual Vulgate manuscripts but notably only in W (19 times), D (13), and V (11). There are 11 apparent corrections to agree with the Vulgate, by first or second hand.

The following changes in order are not supported in the regular sources of the Western or European texts

- 1 10 *albis vestibus* sol.
 21 *sunt congregati* c vg^{ss} Lat(B F K R S U W)
 2 29 *apud nos est* sol.
 43 *fiabant per apostolos* Greek (A C etc.)
 46 *in templo unanimiter* sol, om. *in templo* Gig Perp*, om *unanimiter* D d Lat(S) Greek min
 3 25 *prophetarum estis* sol.
 4 8 *repletus spiritu sancto petrus* vg^{ss} and early editions
 24 *levaverunt vocem unanimiter* Greek (69 242)

- 5.4 *erat in tua potestate sol* , cf d e Gig
 6 *sepelierunt efferentes sol*
 12 *omnes unanimiter sol*
 13 *se coniungere t* vg^{ss} Lat(A M S) cor vat, cf. c
 16 *civitatum vicinarum sol* , cf d *finium undique*
 19 *aperiens ianuas carceris per noctem sol* , cf Lucif om
 per noctem
 20 *huius vitae sol*
 28 *precipiendo vobis precepimus sol*
 istius hominis sol
 42 *non cessabunt in templo et circa domos* vg^{ss}
 6 7 *valde in ierusalem* Lat(O¹), Greek (1898) Sah
 12 *scribas et seniores sol*
 *7 10 *regis pharaonis egipti* Lat(O)
 11 *patres nostri cibos sol*
 14 *patrem suum iacob* Lat(W) Greek (025 049 383 614)
 Syr
 39 *obedire noluerunt sol*
 8.18 *autem vidisset sol* , cf d Lat(C) om *autem*
 9 14 *hic potestatem habet* man 1 (*potestatem hic* corr m 1)
 sol
 33 *ab octo annis sol*
 38 *in ea esset* man 1 sol
 10.3 *nona hora diei* Lat(B F K R S U V)
 9 *in superiora petrus* man 1 sol
 36 *christum iesum sol*
 *37 *per universam iudeam verbum* Lat(W), cf D d om.
 verbum
 38 *deus cum illo erat sol.*
 43 *remissionem accipere per nomen eius peccatorum sol*
 44 *petro loquente sol*
 48 *christi iesu sol.*
 11 7 *vocem et sol*
 12.6 *esset eum* Lat(D R)
 *11 *dominus misit* Lat(Θ*)
 18 *factum esset de petro* vg^{ss} Lat(W)

- 13 11 *manum ei sol*
 13 *pamphilie pergen sol.*
 15 *in vobis est sol.*
 34 *fidelia david* Lat(D S^o U)
 14 1 *multitudo copiosa* man 1 Greek (206 323 337 429 460
 467 489 512 920 927 1522 1831 2298 etc)
 11 *similes hominibus facti* man. 1, sol., cf Lat(D) om.
facti
 15 40 *gratie dei traditus* man 1 sol.
 *16.18 *dixit spiritui* Lat(W)
 26 *statim aperta sunt omnia ostia* c vg^{ss} Lat(B K R S U
 V W)
 28 *nichil tibi feceris mali* Lat(C T)
 17 2 *autem consuetudinem* sol ; cf Greek
 13 *verbum dei a paulo* sol , cf D d om *a paulo*
 16 *civitatem deditam* sol
 18 *stoyci et philosophi* sol.
 19 11 *faciebat deus* cor vat vg^{ss} Greek (H L P S etc), cf
 Lat(W) *deus faciebat deus*
 17 *iudeis omnibus* sol , cf Lat(A Θ) where words stand
 in erasure
 27 *hec autem* sol.
 20 22 *et ecce nunc*, corr man 1, sol.
 36 *oravit cum illis omnibus* sol
 21 2 *phenicem transfretantem* sol.
 9 *quattuor filie* sang¹⁸⁸ vg^{ss} Sah Boh
 11 *manus et pedes* Greek (A 383 614) Sah Chr
 20 *sunt emulatores legis* sol
 22 5 *mihi testimonium* c vg^{ss} Lat(B F K R S U V W)
 *6 *me eunte* = Gig (*michi eunte*) and Greek
 10 *oporteat te* Lat(B F K V W); cf E e om *te*
 11 *illius luminis* sol
 19 *concludens eram* sol
 23 11 *et rome oportet* sol
 24 20 *iudei ex asya* sol
 28 *prestare gratiam* sol.
 25 5 *potentes sunt aut* sol.; cf Lucif Gig Syr om. *aut*, cf.
 Greek (383 614)

- *24 *amplius vivere* c
- *26 2 *apud te beatum*, man 1, Lat(C)
 - 15 *dixit autem dominus* sol
- *25 *sobrietatis et veritatis* Lat(W)
- *28 *fieri christianum* Lat(W)
- 27.19 *armamenta navis suis manibus* Lat(D)
 - 20 *omnis spes salutis* Greek (≠ C H P etc), cf. Gig
 - 30 *inciperent a prora anchoras* c vg^o Lat(B F I K R S U V)
 - 40 *aure flatum* vg^o Lat(B F K R S U V)
- 28 5 *excutiens quidem* sol
 - 25 *spiritus sanctus bene* sol
 - 28 *et ipsi* c vg^o, cf. Gig om *et*, Harcl Syr *enim* for *et*

The examination of the variants not supported in either the *Western* or the *European* text shows many that represent miscellaneous Greek or Latin sources, sometimes in paraphrase. There remains, in addition, the large numbers of unsupported readings noted above, distributed among the same types of variants (additions, word-usage, word-order, omissions, and syntax) which found support in the Old-Latin sources. These may indicate an extension of this general *Western* tradition. Since MS 146 is an English manuscript, these singular readings may in part at least represent an Irish-English Old-Latin text.

SUMMARY

To sum up the study of MS 146 we find that the *Western* sources including Codex Bezae, the African Old-Latin, and the Harclean Syriac give support in 181 variants. If these sources were not fragmentary, they would doubtless support in many more. All except Cyprian agree with our manuscript in all five types of variants. The greatest agreement of all of these sources is found in the long additions.

The study of individual Vulgate manuscripts shows that the older group supports MS 146 in 118 variant readings. These agreements may represent Old-Latin survivals. This

can not, however, be stressed too much, since it is evident that the text of our manuscript also has been adapted to the Vulgate. Some of these agreements may be early Vulgate corruptions rather than Old-Latin survivals.

The so-called *European* sources support our manuscript in 320 variants. Of these G*ig* is complete and P*erp* and E*e* very extensive. The most support is found in the Perpignan manuscript, which in the uncorrected Old-Latin chapters represents almost all known types. The rest of the manuscript shows many survivals of the European-Latin type of text. G*ig*, P*erp*, and L*ucifer* support fairly evenly in all five types of variants, whereas E*e* gives even support in the other types but in only four omissions.

There seems to be an exceptionally close relationship on the part of our manuscript to the European text. The history of the Old-Latin and the Vulgate texts will not, however, warrant our believing that non-Vulgate texts of central Europe influenced texts of Ireland and England. Though it is certain that some influence came from Ireland and England to the continent, it can not account for such extensive agreement in non-Vulgate manuscripts. In the agreements, therefore, between our Irish-English text and the European Latin, it would be wiser to assume that we have in large measure an indication that the African, Old-Irish, and European texts of the Old-Latin go back to closely related sources. However, a not negligible portion of these European variants may have come into MS 146 through the Vulgate manuscript to which its parent was indebted for so many pure Vulgate readings.

Some support is found among miscellaneous sources (Greek Old Uncials, Antiochean text, scattered minuscule manuscripts, Syriac versions, and Latin lectionaries) for variant readings in our manuscript. Though this support is meagre, when not associated with Western or European sources, it furnishes additional evidence for the *Western* influence in MS 146.

There remain 185 unsupported variants, aside from the singular spellings, in MS 146. Most of these are similar in

type to those that have found support in the Old-Latin sources. Therefore many of these unsupported readings may represent an Irish Old-Latin

If the foregoing observations are acceptable, it seems that MS 146 was derived from the original Irish Old-Latin text, which had later been partially corrected to the Vulgate with the aid of a manuscript containing many European and Spanish readings. We must not, however, obscure the fact that this is a conclusion based on four separate proofs: first, that palaeographically MS 146 is English, second, that its text is broadly related to all the representatives of the so-called Western text, including both the Bezan-African and the European Old-Latin, third, that it shows many remarkable agreements with Vulgate manuscripts of Irish or English origin or affiliation, and fourth, that out of its 756 notable variants from the Wordsworth and White Vulgate text, only 261 are found in the later Vulgate text of the Sixtine and Clementine editions.

A COLLATION OF MS 146 WITH WORDSWORTH AND WHITE, NOVUM TESTAMENTUM LATINE

- 1.1 *quidaem*¹ for *quidem*
- 2 *assumptus est* for *adsumtus est*
- 4 *ierosolimis* for *Hierosolimis*
set for *sed*
exspectarent for *expectarent*
add inquit after *audistis*
- 6 *convenerant* for *convenerunt*
- 7 om. *dixit autem eis*
- 8 *set* for *sed*
michi for *mihi*
ierusalem for *Hierusalem*
- 9 *hoc* for *haec*
- 10 *astiterunt* for *adstiterunt*
order = *albis vestibus*
- 11 *assumptus est* for *adsumtus est*
order = *in celum a vobis* (corr. man. 1)

¹ Interchanges of *e* with *ae* and *oe* are common and not noted in the collation

- 12 *ierosolimam* for *Hierosolimam*
 13 *matheus* for *Mattheus*
 14 *hii* for *hi*
 unamiter for *unanimiter* man. 1 (corr man 1)
 15 om *et* before *in diebus*
 exurgens for *exurgens*
 17 *qui* for *quia* .
 19 *ierusalem* for *Hierusalem*
 add *a* before *lingua* (del man 1)
 20 *eius* for *eorum*
 inhabitet for *habitet*
 add *alter* before *alius* (alter del man 1)
 21 *sunt congregati* for *congregati sunt*
 22 *assumptus est* for *adsumtus est*
 resurrectionis for *resurrectionis*
 23 *barsabas* for *Barsabbas*
 mathiam for *Matthiam*
 26 *mathiam* for *Matthiam*
 annumeratus est for *adnumeratus est*
 2 1 *implerentur* for *complerentur*
 add *discipuli* after *omnes*
 2 *tanquam* for *tamquam*
 4 *varius* for *aliis*
 5 *ierusalem* for *Hierusalem*
 om *iudaei*
 7 *loquuntur* for *loquuntur*
 8 *linguam nostram* for *lingua nostra*
 9 om *et* after *Mesopotamiam*
 capadoceam for *Cappadociam*
 asyam for *Asiam*
 10 *frigiam* for *Phrygiam*
 libie for *Lybiae*
 11 *proseliti* for *Proselyti*
 om *nostris* (add man 2)
 13 om *autem*
 irridebant dicentes for *inridentes dicebant* (corr man. 2)
 14 *elevavit* for *levavit*
 ierusalem for *Hierusalem*

- 15 *hui* for *hi*
tercia for *tertia*
- 17 *sompnia* for *somnia*
sompniabunt for *somniabunt*
- 18 om. *super* before *ancillas*
- 21 om. *erit* before *omnis* (add man 1 or 2)
- 22 *approbatum* for *adprobatum*
nobis for *vobis*
- 23 *affligentes* for *adfigentes*
- 25 om. *est* after *a dextris meis*
- 26 *requiescit* (corr *requiescet* man 2)
- 28 *mihi fecisti* for *fecisti mihi*
iocunditate for *iucunditate*
- 29 om. *et* after *quoniam*
order = *apud nos est*
- 31 *resurrectione* for *resurrectione*
videre for *vidit*
- 32 *cui nos omnes testes* for *curus omnes nos testes*
- 34 *ille* for *ipse*
- 36 *igitur* for *ergo*
- 37 *compuncti* for *conpuncti*
- 38 add *domini* after *nomine*
order = *spiritus sancti*
- 40 *verbis plurimis* for *verbis pluribus*
- 41 *apposite* for *adpositae*
order = *in die illa*
iii for *tria* (*a* written above man 2)
- 43 order = *fiebant per apostolos*
ierusalem for *Hierusalem*
- 46 order = *perdurantes in templo unanimiter*
- 47 *collaudantes* for *conlaudantes*
om. *autem* after *dominus*
om. *cotidie* after *fierent* (add man 1 or 2)
- 3 2 *homo* for *vir*
spetiosa for *speciosa*
elemosinam for *elemosynam*
om. *in* before *templum*

- 3 *elemosinam* for *elemosynam* (add *ab eis* man. 2)
 7 *apprehensa* for *adprehensa*
 order = *manu eius*
 allevavit for *adlevavit*
 10 *elemosinam* for *elemosynam*
 spetiosam for *speciosam*
 om. *templi* after *portam* (add man 1 or 2)
 11 *viderunt* for *tenerent* (corr above *vide*, *vel tene* man 2)
 cucurrit for *concurrit*
 12 *polestare* for *pietate*
 13 *ysaac* for *Isaac*
 15 *autorem* (corr man 2 *auctorem*)
 16 *vidistis vos et nostis* for *videtis et nostis*
 17 om *per ignorantiam* (add man 1)
 18 *qui* for *quae*
 add *suorum* after *prophetarum*
 19 order = *peccata vestra*
 20 add *cum* before *venerint* (bracketed in Vulgate)
 nobis for *vobis*
 21 om *quidem* after *celum*
 om *est* after *locutus*
 22 *moyses* for *Moses*
 tanquam for *tamquam*
 23 *quae* for *quaecumque* man 1 (*quaeque* man 2)
 om *non* after *quaeque* (add man. 1)
 24 *annunciaverunt* for *adnuntiaverunt*
 samuel for *Samuhel*
 25 add *autem* after *vos* and order = *vos autem filii*
 prophetarum estis
 nostros for *vestros*
 om *et* before *in semine*
 26 *suscitatis* for *suscitans*
 nequicia for *nequitia*
 4 1 *saducei* for *Sadducaei*
 2 *quid* for *quod*
 annuntiarent for *adnuntiarent*
 resurrectionem for *resurrectionem*

- 3 *in eos manus* for *in eis manus*
 4 *eorum* for *virorum*
 5 *ierusalem* for *Hierusalem*
 6 *cayphas* for *Caiaphas*
 8 order = *tunc repletus spiritu sancto petrus dixit ad eos*
princeps for *principes* man 1 (corr man 3)
 add *audite* after *seniores*
 9 *diudicamur* for *iudicamur*
 10 *votum sit* for *notum sit*
astat for *adstat*
 13 om *et* between *constantiam* and *iohannis* man 1
 (corr man 3)
ammirabantur for *admirabantur*
comperto for *corperto*
 14 *nichil* for *nihil*
 16 *ierusalem* for *Hierusalem*
 17 *comminem* for *comminemur*
 18 *denunciaverunt* for *denuntiaverunt*
nec for *neque*
 19 add *ad eos* after *respondentes*
 21 add *in eo quod acciderat* after *factum fuerat*
clarificabant id quod factum fuerat for *clarificabant*
Deum in eo quod factum erat
 22 *fuerat* for *erat*²
 23 *annuntiaverunt* for *adnuntiaverunt*
 24 order = *levaverunt vocem unanimiter ad dominum*
 om *et* before *mare*
 25 add *in* before *spiritu sancto*
 26 *astiterunt* for *adsteterunt*
 30 *quo* for *cum*
sanctum for *sancti*
 31 add *sunt* after *omnes* (del man 1)
 32 add *unum* after *cor*
et et for *et*
 add *ex his* after *eorum*
set for *sed*

- 33 *resurrectionis* for *resurrectionis*
 add *nostrī* after *dominī*
 order = *dominī nostrī iesu christi*
- 34 *afferebant* for *adferebant*
precia for *pretia*
- 36 om *genere* after *cyprius*
- 37 *precium* for *pretium*
- 5 2 *precio* for *pretio*
afferens for *adferens*
- 3 *temptavit* for *temtavit*
sathanas for *Satanas*
- 4 order = *venundatum erat in tua potestate*
set for *sed*
- 5 *exspiravit* for *expiravit*
audierunt for *audierant*
- 6 *ammoverunt* for *amoverunt*
 order = *et sepelierunt efferentes*
- 7 *spacium* for *spatium*
eius for *ipsius*
- 8 add *mulier* after *Dic mihi*
- 9 add *dixit* after *Petrus autem*
temptare for *temtare*
hostium for *ostium*
- 10 *exspiravit* for *expiravit*
eam for *illam*
- 12 om *autem* after *Per manus*
 order = *omnes unanimiter*
- 13 order = *se coniungere*
set for *sed*
- 15 *in plateis* (corr to *plateas* man. 1)
grabatis for *grabatis*
saltem for *saltem*
illorum for *eorum*
 add *et liberarentur ab infirmitatibus suis* after *illorum*
- 16 om *et* before *multitudo*
 order = *civitatum vicinarum*
ierusalem for *Hierusalem*

- afferentes* for *adferentes*
a for *ab*
- 17 *exurgens* for *exurgens*
saduceorum for *Sadducaeorum*
- 19 order = *aperiens ianuas carceris per noctem*
- 20 order = *huius vitae*
- 21 *in templo* for *in templum*
 add *ministros* after *miserunt*
- 22 *venerunt* for *venissent*
nunciaverunt for *nuntiaverunt*
- 23 *diligencia* for *diligentia*
custodias for *custodes*
- 25 *nunciavit* for *nuntiavit*
- 26 add *templi* (exp man 1) after *magistratus*
- 28 order = *precipiendo vobis precepimus*
ierusalem for *Hierusalem*
 order = *istius hominis*
- 29 order = *oportet obedire*
- 31 *penitenciam* for *paenitentiam*
- 34 *gamahel* for *Gamaliel*
 add *vir* after *honorabilis*
- 35 *attendite* for *adtendite*
- 36 om *dies* after *enim* (add man 2)
 order = *numerus virorum*
nichilum for *nihilum*
- 37 *exstitit* for *extitit*
- 38 om *et* before *nunc*
- 40 add *eis* after *denunciaverunt*
 add *amplius* after *ne*
- 42 order = *non cessabunt in templo et circa domos domos*
docentes (*cessabant* in Vulgate, om *domos*²)
- 6.1 *factum* for *factus*
- 2 *vos* for *nos*
- 3 add *sancto* after *spiritu*
- 4 order = *erimus instantes*
- 5 *procorum* for *Prochorum*
thimonem for *Timonem*

- nicholaum* for *Nicolaum*
anthiochenum for *Antiochenum*
 7 *domini* for *Dei*
 add *erat* after *discipulorum*
 order = *valde in ierusalem*
 8 order = *signa et prodigia*
 11 order = *blasphemie verba*
 moysen for *Mosen*
 12 om *et* before *scribas* and order = *scribas et seniores*
 13 *falsos testes dicentes* for *testes falsos qui dicerent*
 add *blasphemie* after *verba*
 14 *moyses* for *Moses*
 15 add *in* before *eum*
 7 2 *moreretur* for *moraretur*
 4 add *et inde transmigravit illum in terra caldeorum* after
 in charram
 5 *set* for *et*²
 6 add *ei* before *deus*
 semen tuum for *semen eius*
 7 *dicit dominus* for *dixit Deus*
 deservient for *servient*
 8 *gemuit* for *genuit* (corr man 1)
 add *genuit* after *et ysaac* (*Isaac* in Vulgate)
 9 *egiptum* for *Aegyptum*
 10 order = *regis pharaonis egipti*
 egiptum for *Aegyptum*
 11 *super* for *in* before *universam egiptum*
 order = *patres nostri cibos*
 12 *egipto* for *Aegypto*
 13 *manifestum* for *manifestatum*
 14 *patrem suum jacob* for *Iacob patrem suum* (corr.
 man. 2)
 add *suam* after *cognitionem*
 15 *egiptum* for *Aegyptum*
 16 *sichen* for *Sychem*¹
 sepulcro for *sepulchro*
 sichen for *Sychem*²

- 17 *appropinquaret* for *adpropinquaret*
quod for *quam*
egipto for *Aegypto*
- 18 *egipto* for *Aegypto*
- 19 *afflixi* for *adflixi*
 add *nostros* after *patres*
- 20 *moyses* for *Moses*
- 22 *moyses* for *Moses*
egiptorum for *Aegyptiorum*
 om *in* before *operibus*
- 24 *quandam* for *quendam*
 add *de genere suo* after *iniuriam*
facientem for *patientem*
egiptio for *Aegyptio*
- 25 add *suos* after *fratres*
- 26 *in pace* for *in pacem*
- 27 add *suo* after *proximo*
- 28 *egiptum* for *Aegyptium*
- 29 om *moyses* after *autem*
madian for *Madian*
 order = *duos filios*
- 30 om *et* before *expletis annis*
syna for *Sina*
- 31 *moyses* for *Moses*
ammiratus for *admiratus*
 add *ad eum dicens* after *domini*
- 32 add *sum* after *ego*
vestrorum for *tuorum*
ysaac for *Isaac*
 om. *autem*
moyses for *Moses*
- 33 *calciamenta* for *calciamentum*
- 34 *egipto* for *Aegypto*
egiptum for *Aegyptium*
- 35 *moysen* for *Mosen*
 add *super nos* after *iudicem*
- 36 *egipti* for *Aegypti*

- 37 *moyses* for *Moses*
tanquam for *tamquam*
- 38 *sollicitudine* for *solitudine*
- 39 order = *obedire noluerunt*
set for *sed*
 add *eum* after *reppulerunt*
 om. *suis* after *cordibus*
egiptum for *Aegyptum*
- 40 order = *nos precedant*
moysi for *Moses*
huic for *hic*
egipti for *Aegypti*
- 42 add *se* after *autem*
milicie for *militiae*
nunquid for *numquid*
optulistis for *obtulistis*
xl annis for *annis quadraginta*
- 43 *eos* for *eas*
propter hoc in babylonem for *trans Babylonem*
- 44 add *cum* before *patribus*
 add *illis deus* before *loquens*
moysen for *Mosen*
- 48 *set* for *sed*
per prophetam dicit for *propheta dicit*
- 49 *michi* for *mihi* bis
requiescionis for *requietionis*
 om. *est*²
- 51 *dura* for *duri*
incircumcisis cordibus for *incircumcisi cordibus*
restitistis for *resististis*
 add *et* after *sicut*
- 52 add *sunt* after *sunt persecuti*
- 55 add *stephanus* before *plenus*
- 56 order = *stantem a dextris virtutis dei* ;
- 58 *adolescentis* for *adulescentis*
- 60 add *quia nesciunt quid faciunt* after *peccatum*
 add *in domino* after *obdormiuit*

- 8.1 *ierosolimis* for *Hierosolymis*
 2 *stephenum* for *Stephanum*
eum for *illum*
 4 *pertransibant* for *pertransiebant*
 5 add *iesum* after *christum*
 6 *intendebat* for *intendebant*
 add *verba* before *audientes*
 7 *exibant* for *exiebant*
enim for *autem*
paralitici for *paralytici*
 9 *symon* for *Simon*
 om *esse* after *se*
 10 *ascultabant* for *auscultabant*
 11 *attendebant* for *adtendebant*
 om *magicis suis* after *tempore*
 13 *symon* for *Simon*
 om *admirabatur* after *stupens*
 14 *ierosolimis* for *Hierosolymis*
eos for *illos*
 16 *set* for *sed*
 18 order = *autem vidisset*
symon for *Simon*
optulit for *obtulit*
illis for *eis*
 19 *imposuero* for *inposuero*
 20 *possidere* for *possideri*
 21 om. *tibi* after *est* (add above man 1)
 22 *nequicia* for *nequitia*
cogitacio for *cogitatio*
 24 *symon* for *Simon*
nichil for *nihil*
eorum for *horum*
 25 *redibant* for *rediebant*
ierosolimam for *Hierosolymam*
evangelizabant for *evangelizabant*
 26 *ierusalem* for *Hierusalem*
 27 *ierusalem* for *Hierusalem*
eunucus for *eunuchus*

- 28 *ysayam* for *Esaiam*
 30 *accurrens* for *adcurrrens*
 ysaiam for *Esaiam*
 intelligis for *intellegis*
 32 *tanquam* for *tamquam*
 33 *generationes* for *generationem*
 om *quoniam* *tolletur de terra vita eius* (but add in
 marg man 1)
 tolletur for *tollitur*
 34 *eunucus* for *eunuchus*
 35 *a* for *ab* before *scriptura*
 36 *quis* for *quid*
 37 add *Dixit autem philippus. Si credis ex toto corde licet*
 et respondens ait. Credo dei filium esse iesum after
 baptizari.
 38-39 *eunucus* for *eunuchus* bis
 39 *ibat autem* for *ibat enim*
 9.1 om *autem* after *saulus*
 spirans for *aspirans*
 2 *pecuit* (corr to *petiuit* man 1)
 synagogas for *synagogas*
 om *in* before *ierusalem*
 ierusalem for *Hierusalem*
 3 *appropinquaret* for *adpropinquaret*
 5 *at ille* for *et ille*
 add *nazarenus* after *iesus*
 add *Durum est tibi contra stimulum calcitrare et tremens*
 ac stupens dixit Domine, quid me vis facere *Et*
 dominus ad eum after *persequeris.*
 6 om *sed* before *surge*
 8 *nichil* for *nihil*
 9 add *ibi* after *et erat*
 11 *surgens* for *surge*
 12 *introheuntem* for *introeuntem*
 13 *ierusalem* for *Hierusalem*
 14 order = *hic potestatem habet*, corr *potestatem hic habet*
 man 1 (Vulg *hic habet potestatem*)

- 16 order = *eum pati pro nomine meo*
- 17 *illi* for *ei* before *manus*
 order = *dominus iesus misit me*
ut for *et* before *implearis*
- 18 *tanquam* for *tamquam*
- 20 add *ingressus paulus* after *continuo*
sinagogis for *synagogis*
dominum for *Iesum*
- 21 *ierusalem* for *Hierusalem*
- 22 *magis* for *autem multo magis*
invallescebat for *convalescebat*
affirmans for *adfirmans*
- 23 *concilium* for *consilium*
- 24 om *autem* after *custodiebant*
- 25 om *per murum* before *dimiserunt*
submittentes for *summittentes*
- 26 *ierusalem* for *Hierusalem*
temptabant for *temptabant*
quod for *quia*
- 27 *apprehensum* for *adprehensum*
dixit for *duxit* (add *u* supra m 2)
 add *domini* before *iesu*
- 28 *ierusalem* for *Hierusalem*
- 29 *autem gentibus* for *quoque* after *loquebatur*
- 30 add *nocte* after *cesaream* man 1 (tr before *cesaream*
 man 2)
- 31 add *et* before *ecclesia*
 order = *spiritus sancti*
- 32 *transiret* for *pertransiret*
lidde for *Lyddae*
- 33 order = *ab octo annis*
grabato for *crabatto*
paratilicus for *paralyticus*
- 34 *enea* for *Aeneas*
sanet for *sanat*
 add *dominus* before *iesus christus*
- 35 *lidde* for *Lyddae*

- 36 *thabitha* for *Tabita*
elemosinis for *elemosynis*
- 37 om. *autem* after *factum est*
- 38 *lidda* for *Lydda*
 order = *in ea esset* (corr. man. 2)
- 39 *exurgens* for *exsurgens*
eum for *illum*² -
- 40 add *sua* after *genua*
thabita for *Tabita*
 add *in nomine domini nostri iesu christi* after *Tabita*
surge
- 41 *assignavit* for *adsignavit*
- 42 add *iesu christo* after *domino*
- 43 add *per* before *dies multos*
aput for *apud*
symonem for *Simonem*
- 10 2 *familia* for *domo* after *omni*
elemosinas for *elemosynas*
dominum for *Deum*²
- 3 order = *nona hora diei*
- 4 add *in* before *eum*
Quis es for *Quid est*
 om. *tuae* after *elemosine*
- 5 *symonem* for *Simonem*
cognominabat man. 1 (corr. *cognominatur* man. 2)
- 6 *symonem* for *Simonem*
 add *hic dicet tibi quid te oporteat facere* after *iuxta mare*
- 7 *hūs* for *his*
- 9 *appropinquantibus* for *adpropinquantibus*
 order = *in superiora petrus* (corr. man. 1)
 add *domus* after *petrus*
- 10 *illis* for *eis*
- 11 *lintheum* for *lintheum*
submitti for *summitti*
- 13 add *dicens* after *vox ad eum*
- 17 *astiterunt* for *adstiterunt*

- 18 *invocassent* for *vocassent*
symon for *Simon*
hospicium for *hospitium*
- 20 *nichil* for *nihil*
- 22 *accersiri* for *accersire*
- 24 *exspectabat* for *expectabat*
- 25 add *venit* before *cornelius*
- 28 *dixit itaque* for *dixitque*
abominatum for *abominatum*
coniungere for *conungi*
set for *et*
- 29 add *ego* after *ergo* (but delete *man* 1)
accersisti for *accersistis*
- 30 *ad* for *in* before *hanc*
add *ieiunus* before *orans*
coram for *ante*
- 31 *elemosine* for *elemosynae*
- 32 *symonem* for *Simonem*
symonis for *Simonis*
add *is cum venerit loquetur tibi* after *iuxta mare*
- 33 add *ad nos* after *veniendo*
assumus for *adsumus*
transpose *tibi* after *precepta sunt*
- 34 *comperi* for *conperi*
add *suum* after *os*
comperi for *conperi*
- 35 *set* for *sed*
iusticiam for *iustitiam*
- 36 *verbum suum misit dominus filius israhel* for *verbum*
misit filius Israhel
annuntians for *adnuntians*
order = *christum iesum*
- 37 order = *per universam iudeam verbum*
- 38 *transit* for *pertransiit*
order = *deus cum illo erat*
- 39 *regionem* for *regione*
ierusalem for *Hierusalem*

- 40 *tercia* for *tertia*
 41 *set* for *sed*
 resurexit for *resurrexit*
 43 order = *remissionem accipere per nomen eius peccatorum* (corr *peccatorum* after *accipere* man 2)
 44 order = *petro loquente*
 45 *obstupuerunt* for *obstipuerunt*
 46 add *illo* after *loquentes*
 47 *nunquid* for *numquid*
 hi for *hi*
 48 order = *eos baptizari in nomine christi iesu*
 add *apud eos* before *aliquot diebus*
 II.1 add *et honorificabant deum* after *dei*
 2 *adisset* for *ascendisset*
 om. *in* before *ierosolimam* (*Hierosolymam* in Vulgate)
 4 add *per* before *ordinem*
 5 add *vas* after *quoddam* (sic)
 velud for *velut*
 lintheum for *lintheum*
 iiii for *quattuor*
 submiti for *summitti*
 7 order = *vocem et*
 michi for *mihi*
 8 *nunquam* for *numquam*
 9 *mandavit* for *mundavit*
 11 *astiterunt* for *adstiterunt*
 12 *michi* for *mihi*
 nichil for *nihil*
 vi for *sex*
 13 *symonem* for *Simonem*
 15 *cecidit* for *decidit*
 17 *dominum* for *Deum*
 add *ne daret illis spiritum sanctum credentibus in*
 dominum iesum christum after *dominum* ^A
 18 *penitenciam* for *paenitentiam*
 19 order = *que fuerat facta*
 phenicem for *Phoenicen*

- 20 *annuntiantes* for *adnuntiantes*
 22 *ierosolimis* for *Hierosolymis*
 23 *domini* for *Dei*
 permanere proposito cordis sui in domino for *proposito*
 cordis permanere in Domino
 24 *apposita* for *adposita*
 25 add *ad* before *tharsum*
 27 *ierosolimis* for *Hierosolymis*
 28 *famam magnam* for *famem magnam* man 1 (corr.
 man 1)
 29 after *quis* an erasure of two letters, or letter and
 abbreviation mark (*que*)
 in ministerio for *in ministerium*
 12 1 *affligeret* for *adfligeret*
 3 *apposuit ut apprehenderet* for *adposuit adprehendere*
 4 *azimorum* for *Asymorum*
 apprehendisset for *adprehendisset*
 custodiendum for *custodire eum*
 6 order = *esset eum*
 cathenis for *catenis*
 7 *astitut* for *adstitit*
 excitavit for *suscitavit*
 cathenae for *catenae*
 8 *caligas* for *galliculas*
 circunda for *circumda*
 11 order = *dominus misit*
 exspectatione for *expectatione*
 12 *cognominatur petrus marcus* for *cognominatus est*
 Marcus
 13 *ad videndum* for *ad audiendum*
 14 *set* for *sed*
 15 *affirmabat* for *adfirmabat*
 16 add *ostium* after *aperuissent*
 obstupuerunt for *obstipuerunt*
 18 order = *factum esset de petro*
 19 *in* for *a* before *iudea* (corr man 2)
 20 *sydoniis* for *Sidonis*

- 23 *consumptus* for *consumitus*
expiravit for *expiravit*
- 25 *ierosolimis* for *Hierosolymis*
assumpto for *adsumto*
cognominatur for *cognominatus est*
- 13.1 *collectaneus* for *conlactaneus*
- 2 add *autem illis* after *dixit*
segregate michi for *separate michi*
quo for *quod* before *assumpsit* (*adsumsi* in Vulgate)
- 3 *imponentes* for *inponentes*
eos for *illos*
- 4 *seulutiam* for *Seleuciam*
- 5 *salaminam* for *Salamina*
sinagogis for *synagogis*
- 6 *virum magnum* for *virum magum*
barieu for *Bariesu*
- 7 *saulo* for *Paulo*
- 8 *elimas* for *Elymas*
- 10 *iusticie* for *iustitiae*
- 11 om *Domini*
circueus for *circumieus*
order = *manum ei*
- 12 *super doctrina* for *super doctrinam*
- 13 *navigasset* for *navigassent*
add *erant* after *cum eo*
order = *pamphilie pergen* for *Pergen Pamphiliae*
ierosolimam for *Hierosolymam*
- 14 *psidie* for *Pisidiae*
sinagogam for *synagogam*
- 15 *sinagoge* for *synagogae*
order = *in vobis est*
exhortacionis for *exhortationis*
- 18 *per xl annorum* for *per quadraginta annorum*
- 19 *gentes vii* for *gentes septem*
- 20 *l annos* for *quinquaginta annos*
ad samuelem for *ad Samuhel*
- 21 *filium saul cis* for *Deus Saul filium Cis*
annis xl for *annis quadraginta*

- 25 *set* for *sed*
 27 *habitant* for *habitabant*
 ierusalem for *Hierusalem*
 28 *in eo* for *in eum*
 29 *consumassent* for *consummassent*
 30 *tercia* for *tertia*
 31 *ierusalem* for *Hierusalem*
 32 *annunciamus* for *adnuntiamus*
 eam for *ea*
 33 order = *in secundo psalmo* (in marg *quidam codices*
 habent "in primo")
 34 *suscitavit* for *suscitaverit*
 om. *iam* before *non*
 order = *fidelia david*
 35 *alibi ait dicit* for *alias dicit*
 36 add *in* before *sua generatione*
 amministrasset for *administrasset*
 appositus for *adpositus*
 37 *corruptionem* for *corruptionem*
 38 *annuntiatur* for *adnuntiatur*
 moysi for *Mosi*
 41 *contemptores* for *contemtores*
 ammiramini for *admiramini*
 43 *sinagoga* for *synagoga*
 44 *autem* for *vero*
 add *die* before *sabbatho* (exp. man 2)
 dei for *Domini*
 46 *set* for *sed*
 iudicatis for *iudicastis*
 14.1 *iconi* for *in Iconio*
 sinagogam for *synagogam*
 order = *multitudo copiosa* (corr man 2)
 2 add *persecutionem* after *suscitaverunt*
 add *dominus autem pacem cito dedit* after *adversus*
 fratres
 4 add *illius* before *civitatis*
 5 *afficerent* for *adficerent*

- 6 *licaonie* for *Lycaoniae*
listram for *Lystram*
 add *Et commota est omnis multitudo in doctrina eorum.*
Paulus autem et barnabas commorabantur listris after
erant
- 7 *listris* for *Lystris*
- 10 order = *voce magna* (corr to Vulgate man 2)
exiit for *exiuit*
- 11 *licaonie* for *Lycaonice*
 order = *similes hominibus facti* (corr man 2)
- 13 *afferens* for *adferens*
- 14 *concissis* for *conscissis*
- 15 *annuntiantes* for *adnuntiantes*
- 16 add *in* before *vias*
- 17 *leticia* for *laetitia*
- 19 *yconio* for *Iconio*
- 21 *listram* for *Lystram*
ycontum for *Iconium*
- 22 *intrare regnum celorum* for *intrare in regnum Dei*
- 23 om *cum* before *constituissent* (add man 1)
 order = *illis presbyteros per singulas ecclesias*
- 24 *transeuntes autem et pisidiam* for *transeuntesque Pisidiam*
- 27 *congregavissent* for *congregassent*
retulerunt for *rettulerunt*
- 15 1 *moysi* for *Mosi*
salvi fieri for *salvari*
- 2 *seditione paulo* for *seditione non minima Paulo* (corr man 1)
ierusalem for *Hierusalem*
 add *dicebat autem paulus manere eos ita ut crediderunt* after *illos*
ex aliis for *ex illis*
ierusalem for *Hierusalem*
- 3 *pertransibant* for *pertransiebant*
phenicem for *Phoenicen*
conversationem for *conversionem*

- 4 *ierosolimam* for *Hierosolymam*
annuntiantes for *adnuntiantes*
- 5 *crediderunt* for *crediderant*
moysi for *Mosi*
- 8 *illi* for *illis*
- 9 *nichil* for *nihil*
decrevit for *discrevit*
 add *et* before *fide*
- 10 *temptatis* for *temtatis*
- 11 *set* for *sed*
- 14 *simon* for *Simeon*
- 17 *deum* for *Dominum*
- 19 *deum* for *Dominum*
- 20 *set* for *sed*
simulachrorum for *simulacrorum*
- 21 *moyses* for *Moses*
synagogis for *synagogis*
- 22 *barsabas* for *Barsabbas*
- 23 *manum* for *manus*
- 28 *nichil* for *nihil*
- 29 *simulachrorum* for *simulacrorum*
sanguine suffocato (*suffocato* bracketed in Vulgate)
 add *et ea que vobis fieri non vultis alius ne feceritis* after
fornicatione
- 31 add *gaudio magno* after *gavisi sunt*
- 32 add *eos* after *confirmaverunt*
- 33 add *aliquanto* before *tempore*
- 34 add *Visum est autem syle remanere ibi* *Solus autem*
iudas abiit after *illos*
- 37 *assumere* for *adsumere*
- 38 *ut quia* for *qui*
- 39 om *autem* after *facta est*
 add *quidem* after *barnabas*
assumpto for *adsumto*
- 40 *Syla* for *Sila*
gratie dei traditus for *traditus gratiae Domini* (corr
 man 1)

- 41 add *praecipiens custodire praecepta apostolorum et seniorum et cum circumisset* (corr to *circumissent* man. 2) has *nationes* after *ecclesiam* (for *ecclesias* Vulgate)
- 16.1 *listrum* for *Lystrum*
thimotheus for *Timotheus*
- 2 add *bonum* after *testimonium*
listris for *Lystris*
yconio for *Iconio*
- 3 *assumens* for *adsumens*
erat for *esset*
- 4 *pertransissent* for *pertransirent* (corr man 2)
ierosolimis for *Hierosolymis*
- 5 *habundabant* for *abundabant*
- 6 *phrigiam* for *Phrygiam*
 order = *a spiritu sancto*
asya for *Asia*
- 7 *misiam* for *Mysiam*
temptabant for *temptabant*
 add *in* before *bithyniam* (*Bithyniam* in Vulgate)
illos for *eos*
- 8 *misiam* for *Mysiam*
- 9 om. *per noctem* after *visio*
- 10 *quod* for *quia*
- 11 *a trohade* for *a Troade*
samotrachiam for *Samothraciam*
- 12 *prima pars* for *prima partis*
- 14 *liddia* for *Lydia*
thiatirenorum for *Thyatirenorum*
- 16 erasure of two letters before *euntibus*
phitonem for *Pythonem*
- 17 *annuntiant* for *adnuntiant*
nobis for *vobis*
- 18 order = *dixit spiritui*
- 19 *exiit* for *exiit* *
spiritus for *spes* (corr. man. 2)
apprehendentes for *adprehendentes*
sylam for *Silam*

- 20 *hui* for *hi*
 21 *annuntiant* for *adnuntiant*
 add nobis after *annuntiant*
 22 *add eos* after *iusserunt*
 23 *custodirent* for *custodiret* (corr man 2)
 24 *om in* before *ligno*
 25 *sylas* for *Silas*
 26 *ergo* for *vero*
 order = et statim aperta sunt omnia ostia
 28 *order = voce magna*
 order = nichil tibi feceris mali
 29 *add ad pedes* after *syle* (for *Silae*)
 31 *add ei* after *dixerunt*
 in dominum iesum for *in Domino Iesu*
 33 *omnis domus* for *omnes*
 34 *apposuit* for *adposuit*
 37 *indempnatos* for *indemnatos*
 set for *sed*
 etiant for *eciant*
 40 *liddiam* for *Lydiam*
 add narraverunt quanta fecisset dominus cum eis et
 after visis fratribus
 consolantes eos for *consolati sunt eos et*
 17 1 *amphibolim* for *Amphipolim*
 thesalonicam for *Thessalonicam*
 synagoga for *synagoga*
 2 *order = secundum autem consuetudinem*
 3 *order = iesus christus*
 annuntio for *adnuntio*
 4 *syle* for *Silae*
 gentilibus et for *gentilibusque*
 5 *assumentesque* for *adsumentesque*
 assistentes for *adsistentes*
 6 *add et dicentes* after *clamantes*
 6-7 *hui* for *hi* bis
 7 *add nescio quem* after *dicentes*
 9 *accepta satisfactione ab iasone* for *accepto satis ab Iasone*

- 10 *sylam* for *Silam*
venissent for *advenissent*
sinagogam for *synagogam*
- 11 *hui* for *hi*
 add *quemadmodum paulus annuntiaret* after *haberent*
- 12 *et multitudo gentilium mulierum* for *et gentilium mulierum*
- 13 *beroe* for *Beroeae*
 order = *verbum dei a paulo*
 om. *et* before *illuc*
- 14 *cum* for *tunc*
sylas for *Silas*
- 15 add *eum* after *perduxerunt*
sylam for *Silam*
thimotheum for *Timotheum*
- 16 *expectaret* for *expectaret*
 order = *ydolatrie civitatem deditam*
- 17 *sinagoga* for *synagoga*
 om. *et* before *in foro*
- 18 order = *stoyci et philosophi*
seminator verborum for *seminiverbius*
 add *dicebant* after *Alii vero*
annuntiator for *adnuntiator*
resurrectionem for *resurrectionem*
annuntiabat for *adnuntiabat*
- 19 *apprehensum* for *adprehensum*
ariapagum for *Ariopagum*
- 21 *nichil* for *nihil*
discere for *dicere*
- 22 *supersticiosos* for *superstitiosiores*
- 23 *simulachra* for *simulacra*
annuntio for *adnuntio*
- 24 *non manufactis templis habitat* for *non in manu factis templis inhabitat*
- 26 *habitationis* for *habitationis*
- 27 *attractent* for *adtractent*
- 29 *sumus* for *simus*
sculture for *sculpturae*

- 30 *despiciens* for *despiciens*
annuntiat for *adnuntiat*
- 32 order = *cum autem audissent*
irridebant for *inridebant*
- 34 *herentes* for *adhaerentes*
- 18 2 *pontium* for *Ponticum*
 add *paulus et salutavit eos* after *ad eos*
- 3 order = *artis erat*
aput for *apud*
erant for *erat*
- 4 add *et disputabat in synagoga per omne sabbatum*
interponens nomen domini iesu after *scenofactoriae*
artis
- 5 *sylas* for *Silas*
thimotheus for *Timotheus*
 order = *iesum christum*
- 6 *excuciens* for *excutiens*
 add *sua* after *vestimenta*
 add *paulus* before *dixit*
- 7 *synagoge* for *synagogae*
- 8 *archisynagogus* for *archisynagogus*
- 9 *set* for *sed*
- 10 *apponetur* for *adponetur*
- 11 om. *autem* after *sedit*
dicens for *docens*
aput for *apud*
- 12 *insurrexerunt* for *insurrexerunt*
- 13 *credere* for *colere*
 add *in* before *deum*
- 14 add *suum* after *os*
fascinus for *facinus*
- 15 om *et* before *legis*
- 17 *apprehendentes* for *adprehendentes*
percuciebant for *percutiebant*
nichil for *nihil*
- 18 *totonderat* for *totonderant*
- 19 *habeant* for *habebant*
synagogam for *synagogam*

- 21 *set* for *sed*
 add *oportet me solempnem diem facere ierosolimis et*
after et dicens
- 23 *phrigiam* for *Phrygiam*
- 24 *genere* for *natione*
- 26 om. *coepit* after *ergo* (add *cepi* man 1 after *hic*)
sinagoga for *synagoga*
assumpserunt for *adsumserunt*
domini for *Dei*
- 27 *crediderunt* for *crediderant*
- 19 1 *quosdam de discipulis* for *quosdam discipulos*
 2 add *dixerunt* after *illi*
set for *sed*
- 4 *baptismo* for *baptisma*
 om. *populum* after *penitentie* (add man 1)
- 5 add *et cum* after *his* man 2
iesu christi for *Iesu*
- 6 *Cum autem* for *Et cum*
eis manus for *illis manus*
- 8 *sinagogam* for *synagogam*
- 9 add *domini* after *viam*
scola for *schola*
 add *ab hora quinta usque in horam decimam* after
tyranni
- 10 *asya* for *Asia*
dei for *Domini*
- 11 order = *faciebat deus*
- 12 *semicintra* for *semicinctia*
- 13 *templaverunt* for *temptaverunt*
adiuramus for *adiuro*
- 14 add *quidam* after *quidam*
vi filii for *septem filii*
- 17 order = *iudeis omnibus*
- 18 *annuntiantes* for *adnuntiantes*
- 19 *eis* for *his*
hominibus for *omnibus*
precus for *pretiis*
l for *quingenta*

- 21 *ierosolimam* for *Hierosolymam*
 22 *thimotheum* for *Timotheum*
 asya for *Asia*
 23 *om in* before *illo tempore*
 add *domini* after *de via*
 25 *eiusmodi* for *huiusmodi*
 artifitio for *artificio*
 26 add *et* after *set*
 asye for *Asiae*
 order = *turbam multam* (corr. man 2)
 27 order = *hec autem*
 set for *sed*
 nichilum for *nihilum*
 set for *sed*
 asya for *Asia*
 29 *aristarco* for *Aristarcho*
 31 *asye* for *Asiae*
 33 add *quendam* before *alexandrum*
 autem for *ergo*
 36 *nichil* for *nihil*
 38 *proconsules* for *pro consulibus*
 add *se* after *accusent*
 39 *legittima* for *legitima*
 20 1 *convocatis* for *vocatis*
 4 *sosipater* for *Sopater*
 pirri for *Pyrri*
 aristharcus for *Aristarchus*
 thimotheus for *Timotheus*
 asyam for *Asiani*
 tuticus for *Tychicus*
 5 *hui* for *hi*
 sustinuerunt for *sustinebant*
 6 *aximorum* for *Axymorum*
 diebus vii for *diebus septem*
 7 *om. in* before *una*
 venissemus for *convenissemus*
 add *cum* before *eis*
 add *protexit* before *protraxitque* (exp. man. 1)

- 9 *adolescens* for *adulescens*
euthicus for *Eutyclus*
ductus sompno for *eductus somno*
tercio for *tertio*
et sublatus oblatuſ est mortuus for *et sublatus est mortuus*
- 11 *accedens* for *ascendens*
panem gustansque satis allocutus est for *panem et gustans satisque allocutus*
in lucem for *ad lucem*
 add *et* before *sic*
- 13 *vero* for *autem*
navigavimus for *enavigavimus*
- 14 *invenisset* for *convenisset*
assumpto for *adsumto*
mytilenaem for *Mytilenen* man. 1 (*mytilenem* corr man. 1)
- 15 *applicuimus* for *adplicuimus*
- 16 *asya* for *Asia*
ierosolimis for *Hierosolymis*
- 18 *asiam* for *Asiam*
- 19 *humilitate et mansuetudine et lacrimis et temptationibus*
 for *humilitate et lacrimis et temptationibus*
- 20 *nichil* for *nihil*
annuntiarem for *adnuntiarem*
- 21 *per* for *in* before *dominum*
- 22 order = *et ecce nunc* (corr to Vulgate man 1)
ierusalem for *Hierusalem*
- 23 *michi* for *mihi*
- 24 *set* for *sed*
nichil for *nihil*
preciosiore for *pretiosiore*
consumem for *consummem*
 add *verbi* after *ministerium*
accepit for *accepi* (corr man 1) *
- 26 add *vestrum* after *omnium*
- 27 *annuntiarem* for *adnuntiarem*

- 28 *attendite* for *adtendite*
 29 *dissessionem* for *discessionem*
 rapaces for *graves* after *lupi*
 30 *exurgent* for *exsurgent*
 33 *et* for *aut*¹
 35 *beatus** for *Beatus*
 36 order = *oravit cum illis omnibus*
 21 1 *chorum* for *Cho*
 add *deinde in hyram* after *patharam* (*Patara* in Vulgate)
 2 *in phenicem transfretantem* for *transfretantem Phoenicem*
 3 *apparuissemus* for *paruissemus*
 om *et* after *cypro*
 4 *vii* for *septem*
 ierosolymam for *Hierosolymam*
 5 *expletis* for *explicitis*
 in littore for *in litore*
 7 *ptolomaidam* for *Ptolomaida*
 aput for *apud*
 8 om. *in* before *domum*
 add *unus* before *de septem*
 aput for *apud*
 or
 9 order = *iii filie*
 11 order = *manus et pedes*
 order = *iudaei in ierusalem*
 12 *ierosolimam* for *Hierosolymam*
 13 *set* for *sed*
 ierusalem for *Hierusalem*
 14 *sudere* for *suadere*
 15 *ierusalem* for *Hierusalem*
 16 *cesareano* for *Caesarea*
 add *secum* after *adducentes*
 aput for *apud*
 iasonem for *Mnasonem*
 17 *ierosolimam* for *Hierosolymam*
 18 om. *nobiscum* after *paulus* (add man. 1)

* *Beat*^s may indicate *Beatus* Cf. 27 34.

- 20 *et* for *at*
 order = *omnes sunt emulatores legis*
- 21 *moyse* for *Mose*
- 23 om. *tibi* after *quod*
nobiscum for *nobis*
 or
iiii for *quattuor*
- 24 *assumptis* for *adsumtis*
set for *sed*
- 26 *assumptis* for *adsumtis*
cum eis for *cum illis*
annuntians for *adnuntians*
unquoque for *unoquoque*
- 27 *vii* for *septem*
consumarentur for *consummarentur*
hii for *hi*
de asya for *ab Asia*
- 28 add *nos* after *adiuvate*
 om. *populum* after *adversus* (add man. 2)
- 29 *introduxis* for *introduxisset*
- 30 *apprehendentes* for *adprehendentes*
- 31 *ierusalem* for *Hierusalem*
- 32 *assumptis* for *adsumtis*
decurrit for *decucurrit*
- 33 *apprehendit* for *adprehendit*
cathenis for *catenis*
- 37 om. *cum* before *cepisset*
- 38 *egyptius* for *Aegyptius*
 om. *in desertum* after *eduxisti* (add man. 1)
 or
iiii for *quattuor*
- 39 *siccariorum* for *sicariorum*
- 40 *et manu* for *et magno*
- 22 2 *loqueretur* for *loquitur*
- 3 *cilitie* for *Ciliciae*
gamalielis for *Gamaliel*
 om. *legis* after *emulator*

- 5 order = *mihi testimonium*
ierusalem for *Hierusalem*
- 6 order = *me eunte*
appropinquante for *adpropinquante*
- 7 *michi* for *mihi*
 add *Durum est tibi contra stimulum calcitrare* after
persequeris
- 10 order = *que oporteat te facere*
- 11 order = *illius luminis*
- 13 *astans* for *adstans*
- 14 om *ex ore* after *vocem* (add man 2)
- 16 *exurge et baptizare et abluere* for *exsurge, baptizare, et ablue*
- 17 order = *mihi revertenti*
ierusalem for *Hierusalem*
in templum for *in templo*
- 18 *ierusalem* for *Hierusalem*
- 19 order = *concludens eram*
sinagogas for *synagogas*
- 20 *astabam* for *adstabam*
- 21 *ad nationes* for *in nationes*
- 22 om *eum* after *autem*
 om *suam* after *vocem*
huiusmodi for *eiusmodi*
- 24 *fragellis* for *flagellis*
acclamarent for *adclamarent*
- 25 *astrinxisset* for *adstrinxissent*
astanti for *adstanti*
indempnatum for *indemnatum*
- 26 add *ei* after *nuntiavit*
- 27 *Dic mihi si tu romanus es* for *Dic mihi, tu Romanus es?*
- 28 *civilitatem* for *civitatem*
- 29 *ligasset* for *alligasset*
- 23 2 *astantibus* for *adstantibus*
- 3 *percuciet* for *percutiet*
- 4 *astabant* for *adstabant*
- 6 *sacerdotum* (-ce-after *sa* del. man 1) for *Sad-
 ducaeorum*
 add *de* before *resurrectione*

- 7 *saduceos* for *Sadducaeos*
- 8 *saducei* for *Sadducaei*
resurrectionem for *resurrectionem*
 add *sanctum* before *spiritum* man. 2
- 9 om. *autem* after *Factus est*
exurgens for *surgentes*
nichil for *nihil*
- 10 *ab eis paulus* for *Paulus ab ipsis*
 om. *de medio eorum, ac deducere eum* before *in castra*
- 11 *assistens* for *adsistens*
 add *in* before *ierusalem*
 order = *te et rome oportet testificari*
- 13 *xl* for *quadraginta*
 add *viri* after *xl*
- 14 *ad principem* for *ad principes*
nichil for *nihil*
- 15 *consilio* for *concilio*
adducat for *producat*
tanquam for *tamquam*
appropriet for *adpropriet*
- 16 *introiit* for *intravit*
- 17 *adolescentem* for *adulescentem*
- 18 *assumens* for *adsumens*
adolescentem for *adulescentem*
ostendere tibi for *loqui tibi*
- 19 *apprehendentes* for *adprehendentes*
manus for *manum*
eius for *illius* (corr. man. 1)
- 20 om. *te* after *rogare*
perducas paulum for *Paulum producas*
- 21 add *quam* after *amplius*
xl for *quadraginta*
illum for *eum* after *interficiant*
exspectantes for *expectantes*
- 22 *adolescentem* for *adulescentem*
- 23 *convocatis* for *vocatis*
cc for *ducentos*

- lxx* for *septuaginta*
cc for *ducentos*
tercia for *tertia*
24 *imponentes* for *inponentes*
add *eum* after *paulum*
25 add *timuit enim ne forte raperent eum iudaei et occiderent*
et ipse postea calumpniam sustineret quasi pecuniam
accepturus after *presidem*
add *ei* after *scribens*
add *verba* before *haec*
29 *nichil* for *nihil*
30 *paraverant* for *paraverunt*
add *eum* after *miri*
apud for *apud*
31 *assumentes* for *adsumentes*
32 *in* for *ad* before *castra* (corr *ad* man 2)
33 *epistolam* for *epistulam*
34 *provincia* for *provincia*
add *esset* after *cilitia*
35 om *et* before *accusatores*
24 1 *aratore* for *oratore*
audierunt for *adierunt*
2 *accito* for *citato*
3 *semper hec utique suscepimus* for *semper et ubique*
suscipimus
6 *quia* for *qui*
7 add *voluimus secundum legem nostram iudicare super-*
veniens autem tribunus lysias cum vi magna eripuit
eum de manibus nostris iubens accusatores eius venire
ad te after *apprehensum* (for *adprehendimus* Vulgate)
10 *satisfaciam* for *satis faciam*
11 *michi* for *mihi*
xii for *duodecim*
ierusalem for *Hierusalem*
12 *sinagogis* for *synagogis*
14 *deservio deo patri meo* for *deservio patri Deo meo*
15 *hii* for *hi*
exspectant for *expectant*

- 16 *consciam* for *conscientiam*
 17 *elemosinas* for *elemosynas*
 in gentes meas for *in gentem meam*
 19 add *et apprehenderunt me clamantes et dicentes* *Tolle*
 inimicum nostrum after *cum tumultu*
 20 order = *iudei ex asya*
 add *modo* before *apud te*
 accusarent for *accusare*
 21 *hui* for *hi*
 invenerint for *invenerunt*
 22 *resurrectione* for *resurrectione*
 24 *custodire* for *custodiri*
 quenquam for *quemquam*
 25 order = *Post autem aliquot*
 add *dominum* before *iesum*
 26 *iusticia* for *iustitia*
 add *enim* before *autem* (del *man. 1*)
 tremefactus for *timefactus*
 28 *porticum* for *Porcium*
 order = *prestare gratiam*
 25 1 *ierosolimam* for *Hierosolymam*
 3 add *in* before *ierusalem*
 4 add *quidem* before *paulum*
 5 order = *potentes sunt aut*
 7 om *cum* after *Qui*
 ierosolima for *Hierosolyma*
 add *ei* after *obicientes*
 8 om *autem* after *paulo*
 in lege for *in legem*
 9 *ierosolimam* for *Hierosolymam*
 apud for *apud*
 11 *nichil* for *nihil*
 hui for *hi*
 13 *beronice* for *Bernice*
 14 *ibidem morarentur* for *ibi demorarentur* *
 15 *ierosolimis* for *Hierosolymis*
 dampnationem for *damnationem*

- 16 *donec* for *priusquam* (exp and add *priusquam* in marg man. 2)
 add *quae ei obiciuntur* after *crimina*
- 19 om *vero* after *questiones*
supersticione for *superstitione*
affirmabat for *adfirmabat*
- 20 *ierosolimam* for *Hierosolymam*
- 21 *servare* for *servari*
- 22 add *dixit* after *autem*
 add *respondens festus* after *audire*
- 23 om *et* before *iubente*
beronice for *Bernice*
 om. *et* before *iubente*
- 24 *vobiscum* for *nobiscum*
ierosolimis for *Hierosolymis*
et acclamantes for *et hic clamantes*
 order = *amplius vivere*
- 25 *nichil* for *nihil*
- 27 *causam* for *causas*
- 26 2 order = *me apud te beatum* (corr man 1)
 3 *apud* for *apud*
 add *te* after *apud* (del man. 1)
pacienter for *patienter*
- 4 *ierosolimis* for *Hierosolymis*
- 6 *subnectus* for *subiectus*
- 7 *xii* for *duodecim*
servientes for *deservientes*
- 8 *qui* for *quid*
apud for *apud*
- 10 *ierosolimis* for *Hierosolymis*
- 11 *sinagogas* for *synagogas*
compellebam for *conpellebam*
- 14 *michi* for *michi*
hebrayca for *Hebraica*
- 15 order = *Dixit autem dominus*
- 16 *set* for *sed*
exurge for *exsurge*

- 17 *de populis* for *de populo*
 18 *sathane* for *Satanae*
 19 *celesti visioni* for *caelestis visionis*
 20 *set* for *sed*
 ierosolimis for *Hierosolymis*
 per for *in* before *omnem regionem*
 annuntiabam for *adnuntiabam*
 21 add *volentes me* after *temptabant*
 22 *nichil* for *nihil*
 locuti for *locuti*
 om. *sunt* before *locuti* (for *locuti*)
 moyses for *Moses*
 23 *resurrectione* for *resurrectione*
 annuntiaturus for *adnuntiaturus*
 25 *et* for *at*
 set for *sed*
 order = *sobrietatis et veritatis*
 26 *enim enim* for *enim*¹
 nichil for *nihil*
 28 add *inquit* and order = *In modico inquit suades me*
 fieri christianum
 29 add *ait* after *opto*
 aput for *apud*
 set for *sed*
 om. *hos* before *qui audiunt*
 30 *exurrexit* for *exsurrexit*
 beronice for *Bernice*
 assidebant for *adsidebant*
 31 *Qui cum* for *Et cum*
 nichil for *nihil*
 27.1 *tradiderat* for *et tradi*
 2 *hadrimetinam* for *Hadrumetinam*
 et incipientes for *incipientem*
 asye for *Asiae*
 aristharco for *Aristarcho*
 thessolonicense for *Thessalonicense*
 3 *sydonem* for *Sidonem*

- 4 add *nos* after *sustulissemus*
cyprum for *Cypro*
- 5 *cylicie* for *Ciliciae*
add *xv diebus* after *navigantes*
licie for *Lyciae*
- 6 order = *inveniens navem centurio*
- 7 *iuxta salmonem* for *secundum Salmonem*
- 8 *boniportus* for *Boni portus*
thesalia (*s* written above *s* man 1) for *Thalassa*
- 10 *dampno* for *damno*
set for *sed*
vestrarum for *nostrarum*
- 11 *nauclero* for *nauclerio*
- 12 *yemandum* for *hiemandum*
phenicem for *Phoenicen*
yemare for *hiemare*
add *aptum* before *portum*
affricum for *Africum*
- 13 *aspirante* for *adspirante*
- 15 *arepta* for *arrepta*
- 17 *submisso* for *summisso*
- 18 *valde* for *valide*
- 19 *tercia* for *tertia*
order = *armamenta navis suis manibus*
- 20 add *neque luna* after *autem*
order = *omnis spes salutis*
- 21 add *me* after *quidem*
anchora for *a Creta* (add *a creta* above, man 2)
- 23 *astitit* for *adstitit*
- 24 *assistere* for *adsistere*
- 25 *deo meo* for *Deo*
- 27 *set* for *sed*
add *die* after *decima*
- 28 *qui et submittentis bolidem* for *qui summittentes*
xx for *viginti*
xv for *quindecim*

- or
 29 *iii* for *quattuor*
 30 *optentu* for *obtentu*
 order = *quasi inciperent a prora anchoras extendere*
 31 om *hi* after *nisi*
 32 *abscidere* for *excidere*
 33 *assumere* for *sumere* (as- del man 2)
 expectantes for *expectantes*
 nichil for *nihil*
 34 *sumere* for *accipere*
 *nullus*¹ for *nullius*
 36 *assumpserunt* for *adsumserunt*
 37 *in navi numero ducente lxx sex* for *in navi ducentae*
 septuaginta sex
 38 *saciati* for *satiati*
 alleviabant for *adleviabant*
 39 *facta* for *factus*
 40 *sustulissent* for *abstulissent*
 order = *secundum aure flatum*
 43 add *in mare* after *mittere se*
 28 1 *mitilene* for *Militene*
 vocabatur for *vocatur*
 2 *pirra* for *pyrra* (first *r* del man 2)
 ymbrem for *imbrem*
 3 *imposuisset* for *inposuisset*
 4 *in manu* for *de manu*
 5 order = *ille excutiens quidem*
 nichil for *nihil*
 6 *in timorem* for *in tumorem* (corr. to Vulgate man. 1)
 illis expectantibus for *illis sperantibus*
 nichil for *nihil*
 convertantes for *convertentes* (corr to Vulgate man. 1)
 8 *dissenteria* for *dysenteria*
 10 add *nobis* before *imposuerunt*
 11 *vero* for *autem*
 yemaverat for *hiemaverat*
 castrorum for *Castorum*

¹ *null* here probably for *nullius* Cf 20 35.

- 12 *syracusam* for *Syracusas*
aput for *apud*
- 14 *vii* for *septem*
- 15 add *appii* after *fratres*
 om *appii* before *forum*
tribus tabernas for *Tribus Tabernis* (corr man 2)
- 16 add *ipsi foris extra castra* after *sibimet*
- 17 *tercium* for *tertium*
nichil for *nihil*
ierosolimis for *Hierosolymis*
- 18 add *alia* after *nulla*
 order = *mortis esset*
- 20 *cathena* for *catena*
- 22 *rogavimus* for *rogamus*
- 23 *hospicium* for *hospitium*
eis de iesu for *eos de Iesu*
moysi for *Mosi*
- 25 order = *quia spiritus sanctus bene*
ysaiam for *Esaiam*
- 26 add *ad eos* after *dicit*
intelligetis for *intellegetis*
- 27 om *enim*
intelligent for *intellegant*
eos for *illos*
- 28 order = *et ipsi*
- 29 add *Et cum hec dixisset egressi sunt iudei multam inter*
se habentes questionem after *audient*
- 30 add *disputans* after *in suo conducto*
 add *iudeos atque grecos* after *ad eum*
- 31 om. *Amen*
 om *Explicit Actus Apostolorum*

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THE SEGREGATION OF SULFUR AND DWARF FROM CROSSES INVOLVING *OENOTHERA FRANCISCANA* AND CERTAIN HYBRID DERIVATIVES¹

BRADLEY MOORE DAVIS

ABSTRACT

This is a study of segregation for the most part concerned with two characters (1) flower color whether yellow, *S*, or sulfur, *s*, and (2) stature whether tall, *D*, or dwarf, *d*. Segregation was fully expressed but the ratios in certain cases showed marked deficiencies of sulfur and to a less degree dwarf.

Style cutting experiments on monohybrids from homozygous parents clearly indicated slower growth of *s* pollen tubes but not of *d* tubes. There were, however, some cultures in which the deficiency of sulfur must be laid to possible competition among megaspores, female gametophytes or developing seeds.

The segregation from dihybrids out of homozygous parents gave the expected classes but sulfur plants and dwarfs were far below expectations and the combination sulfur dwarf suffered more than either sulfur tall or yellow dwarf. The general conclusion may be drawn that the *SD* gametophytes and gametes function much more frequently than the others and the *sd* gametes least frequently of all. The differential factor is not wholly rate of pollen tube growth nor wholly competition among megaspores and female gametophytes and embryos. A factor in common may be that of physiological vigor most strongly expressed through the association of the two dominants, *S* and *D*, in the class yellow tall, less strongly expressed when only one dominant, *S* or *D*, is present, and least of all through the association of *s* and *d* in the double recessive, sulfur dwarf.

Other sets of crosses concerned two types, yellow and sulfur, heterozygous for green buds dominant over red buds. They were plants with chromosomes in a circle of 12 and one pair in contrast to the all pairing chromosomes of the previous types. Green buds are linked to tall stature and carry a lethal which prevents their inheritance through the pollen. Crosses of these two types to one another and to the homozygous *franciscana* offered peculiarities of segregation with frequent deficiencies of sulfur. Sparse pollination sometimes improved the proportions of sulfur and sometimes worked to its disadvantage. Doubts arise as to the value of experiments on sparse pollinations in relation to problems of slower pollen tube growth. Sparse pollinations give small capsules and high proportions of sterile seeds, suggesting irregularities of normal physiology that might modify the competition that must be present between female gametophytes and embryos. Style cutting experiments in certain cases presented clear evidence of a slower growth on the part of *s* and *d* pollen tubes whatever other factors may be present to confuse the situation.

¹ Genetical Studies on *Oenothera* XVIII. Papers from the Department of Botany, University of Michigan, No. 591.

Crossovers affecting green buds in their linked relations to tall stature are described from various material. The resultant types tall reds were not infrequent in certain cultures but their companion forms dwarf greens appeared rarely and proved to be weak plants.

INTRODUCTION

For some ten years I have gathered data on the inheritance of three characters in *Oenothera franciscana* Bartlett in contrast with allelomorphs in a series of derivatives involving an original cross *biennis* \times *franciscana*. The characters are (1) petal color whether the yellow of *franciscana* or sulfur, (2) height whether tall (9 dm.) as in *franciscana* or dwarf (5 dm.), and (3) color of bud cones whether wholly green (early in the flowering season) or red.

Yellow flowers are dominant to sulfur, tall stature to dwarf, and green buds to red. For these characters the following symbols will be used. *s* for sulfur and *S* for yellow (Renner, 1925), *d* for dwarf and *D* for tall (Emerson, 1931a), *g* for red buds and *G* for green buds corresponding to *gr* and *Gr* of Emerson. The *d* for dwarf stands for a different gene from the *n* of *nanella* as established by Emerson (1931b, p. 389) through a cross between sulfur dwarf and *nanella*. The *G* for green buds is probably an allelomorph in the *P* series of Renner (1925) based on punctuate stems, but with dominance reversed from that found in *Lamarckiana*. Since plants homozygous for green buds have not appeared in my material it has been impossible to follow the punctuate character and for present purposes it has seemed best to express the situation in this simple manner.

In the course of the study four homozygous types have been established and carried along in pure lines, each carrying 7 pairs of chromosomes.

- A Yellow tall red buds. *Oenothera franciscana* Bartlett
^h*franciscana* . ^h*franciscana* *SSDDgg*
- B Sulfur tall red buds. A true *O. franciscana sulfurea*.
^s ^h*franciscana* . ^s ^h*franciscana* . *ssDDgg*.
- C Yellow dwarf red buds. *O. franciscana nana*
^h ^h*franciscana* . ^d ^h*franciscana* . *SSddgg*

D Sulfur dwarf red buds *O franciscana sulfurea nana*
 s d ^hfranciscana . s d ^hfranciscana ssddgg.

In addition two heterozygous types have been segregated and maintained through appropriate selection in selfed lines. In my material each carries a circle of 12 chromosomes and one pair

E Yellow tall green buds. d ^hfranciscana sulfurens
SsDĠGġg.

F. Sulfur tall green buds. The "*franciscana sulfurea*" of
 genetical literature. s d ^hfranciscana . sulfurens
ssDĠGġg

The following types which complete the possible combinations have appeared, but it has been impossible to carry them on in selfed lines. The plants are physiologically weak and green budded segregates frequently fail to develop, selfing giving only a progeny of dwarf reds.

G. Yellow dwarf green buds. d ^hfranciscana d sulfurens
SsdĠGġg.

H. Sulfur dwarf green buds s d ^hfranciscana d sulfurens.
ssdĠGġg

Throughout the studies clear-cut segregation from appropriate crosses was easily established, but the ratios presented were anomalous in that dwarfs in numbers were frequently not up to expectations and there were marked deficiencies of sulfur plants. Peculiarities of breeding in certain material were due to the fact that the gene *G* is only carried through the egg, a pollen lethal preventing its inheritance through the sperm.

The paper will give first the history of the types and their behavior in line breeding. There will then follow the results from cross breeding which determine the correctness of the genetical formulæ given above. Experiments such as have been carried out by Correns, Heribert-Nilsson, Renner, Hiorth and others, which deal with competitive growth of pollen tubes (certation), will be described in relation to anomalies of segregation. An account of crossovers will present data of some interest.

Cultures representing complete germination were from seeds subjected while in water to pressure, generally of about 30 pounds, alternating with exhaust. The operations were performed about five times in 24 hours after which the seeds were spread over wet filter paper in Petri dishes. By this treatment water seems to be forced through the seed coats and germination starts at once, giving almost complete germination within a week. The seedlings before shedding their seed coats were removed from the first Petri dishes to others where they remained until large enough to be set in flats. The residues of ungerminated seeds were usually empty of contents.

TYPE A YELLOW, TALL, RED BUDS, *O. franciscana*;
SSDDgg; TABLE I

This line of *Oenothera franciscana* Bartlett is descended from a plant in Bartlett's culture of 1912. Descriptions and figures have been published (Davis, 1916) and the line is carried in my garden as *franciscana* B to distinguish it from another line, *franciscana* D, synthesized by selfing a haploid. I have carried the line *franciscana* B through 17 generations with a total of 6838 matured *franciscana* plants. Pollen is perfectly formed, which means that less than 1 per cent of the grains are shriveled, and seed germination is close to 90 per cent. The line has bred true except for the few variants recorded in Table 1 where data on the larger cultures grown from seed forced to complete germination are given. The most interesting sport from the line is the haploid (Davis and Kulkarni, 1930) which was first noted in the culture of 1923 and later appeared in the large cultures of 1927 and 1928. The other sports were occasional dwarf rosettes and the form named bushy dwarf. A culture (28.33) from bushy dwarf gave 144 *franciscana* and 29 bushy dwarfs, germination 49.4 per cent, indicating that the dwarf was a trisomic type. It was probably the plant later studied by Anderson (1933).

Table 2 gives the results of a set of selfings where less pollen was applied to the stigma than could satisfy the

number of ovules in the ovary. They were, therefore, experiments in sparse pollination and would give opportunity for any slower growing pollen tubes to function that otherwise

TABLE 1

TYPE A CULTURES OF *Oenothera franciscana* FROM SEEDS FORCED TO COMPLETE GERMINATION, YELLOW, TALL, RED BUDS, SSDDgg

Culture	Seeds	Seedlings	Per cent germination	Mature franciscana	Franciscana-like rosettes	Other forms	Died
21.21	1634 (3 capsules)	1425	87.2	1352	21		52
23.21	505 (1 capsule)	369	73.1	176		1 haploid	192
27.21	1431 (3 capsules)	1146	80.1	1107	3	1 haploid 6 bushy dwarfs 1 narrow-leaved dwarf rosette 1 broad-leaved dwarf rosette	27
27.25	447 (1 capsule)	375	83.9	351		4 bushy dwarfs 1 thick-leaved dwarf rosette	19
28.61	885 (2 capsules)	855	96.6	844		1 haploid 1 bushy dwarf 1 dwarf rosette	8
29.61	837 (2 capsules)	762	91	740			22
30.61	384 (1 capsule)	364	94.8	356			8

might be cut out in competition with normal grains. The selfings gave capsules much smaller than the normal which measure 28–30 mm. long and carry from 350 to 450 seeds. Three triploids appeared in the cultures from the smallest capsules. Pollen deficiency did not bring out variants more numerous than do full pollinations and gave no suggestion of the presence of pollen grains genetically different from the usual.

The pollen grains of *franciscana* contain minute spindle-shaped starch grains of apparently only one type. The readiness with which the grains germinate in secretions of the stigma may be tested by dusting the pollen lightly over

TABLE 2

CULTURES OF *Oenothera franciscana* FROM SEED DEVELOPED IN SMALL CAPSULES AS THE RESULT OF SPARSE POLLINATIONS
Normal capsules measure 28-30 mm long

Culture	Length of capsule	Seeds	Seedlings	Per cent germination	Mature <i>franciscana</i>	<i>Franciscana</i> -like rosettes	Other forms	Died
24 21a	14 mm	283 (3 capsules)	112	39.6	74	1	3 triploids	34
24 21b	20 mm	136 (2 capsules)	134	99.2	127			7
24 21c	24 mm	375 (2 capsules)	356	94.9	309		1 dwarf, probably haploid	46

smears of the secretions on slides, and putting the slides in a moist chamber. At favorable temperatures long pollen tubes are developed after 4 to 6 hours. Data are given below on the percentage of germination of *franciscana* pollen (A) in its own secretion and in the secretion of type E, a heterozygous plant of very different genetical constitution.

	Full grains germinating	Full grains failing to germinate	Per cent germination	Empty and shriveled grains
Pollen A in secretion A	155	86	64.3	1
Pollen A in secretion E	174	72	70.7	5
	329	158	67.5	6

It will be noted that the percentages of germination were not high, but they probably underrate the viability of the pollen since it is not likely that all of the pollen grains spread over a smear will come in sufficiently close contact with the secretion to germinate.

TABLE 3
THE LINE OF SYNTHESIZED *franciscana* D DERIVED FROM THE HAPLOID SELFED

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Mature <i>franciscana</i>	<i>Franscasea</i> -like rosettes	Other forms	Died
29.41	23 21-165 The first haploid selfed	886 (3 capsules)	847	95.6	808		1 dwarf	38
30.22	29.41-4 <i>franciscana</i>	870 (2 capsules)	831	95.5	818		2 haploids 1 dwarf rosette	10
31.22	30.22-788	995 (3 capsules)	966	97.1	773		2 dwarfs	191
32.22	31.22-280	1115 (3 capsules)	999	89.6	821		1 haploid	177
33.22	32.22-926 Pollen 80 per cent good	856 (3 capsules)	773	90.3	579	87		107
35.22	33.22-25 Pollen 90 per cent good	250 (1 capsule)	233	93.2	123	24		86

Table 3 gives some pertinent data on the line *franciscana* D synthesized by selfing the first haploid to appear (23.21-165). The plants of the earlier generations had the strong central shoots and the perfect pollen characteristic of *franciscana* B, but in the fourth generation the pollen of some plants was found to be only 80 per cent good and culture 33.22 was grown from seed of one of these plants. Most of the plants in this culture failed to develop central shoots, thus exhibiting a sprawling habit, and pollen of 68 samples gave percentages of good pollen ranging from 20 to 90, with intermediate grades. Culture 35.22 from a plant with pollen 90 per cent good gave a worse performance, 46 plants with central shoots and 77 without, and pollen from 28 samples ranged from 15 to 85 per cent good. A high mortality in the later generations indicates decreasing vigor. It would seem that my line *franciscana* D has changed materially from what it was at the start. Kulkarni (1931), as would be expected, found the line carried 7 pairs of chromosomes at the time of its origin in 1930.

The cytology of *franciscana* has been the subject of careful study. Cleland (1922) from material in my cultures of 1919-20 first described at diakinesis a circle of 4 chromosomes and 5 pairs. From *franciscana* in Shull's garden of 1925, derived from my line, Cleland (1928) reported 7 pairs. Sturtevant (1931) from material out of my line, received in 1925, lists *franciscana* as having 7 pairs. My tests of parent plants in the line have shown it to be carrying 7 pairs in 1928, 1933 and 1935. The records of Cleland show that the parent plant (20.21-5) of the generation grown in 1921 had the circle of 4 chromosomes. It is therefore clear that the later plants of the line with 7 pairs of chromosomes were descended from a plant with the circle of 4 and 5 pairs as a result of the mating of gametes with the same chromosome configurations.

For the purposes of this paper it should be borne in mind that the present *franciscana* of the line has all pairing chromosomes and is homozygous for yellow flowers, tall stature, and red buds, *SSDDgg*.

TYPE B SULFUR, TALL, RED BUDS, *O. franciscana*
sulfurea, *ssDDgg*, TABLE 4

At this point we must correct a misnomer which came into the *Oenothera* literature through an early paper (Davis, 1916, p. 243), and which has continued with publications of Cleland, Emerson, Shull and others. The name *sulfurea*, as an implied variant from *franciscana*, was first given by me to a plant (14 56 w) with sulfur flowers, tall stature and green buds which appeared in the F_2 of a cross *biennis* \times *franciscana*. It is the plant to be considered under the heading F of this paper and with the genetical formula later established to be *ssD \widehat{G} g \widehat{g}* . At the time when this form first appeared in my garden it was not understood that green buds are not found in races of *franciscana* and that in this material green buds are allelomorphic to and dominant over red buds. Later when certain peculiarities of its breeding were established it became clear that the name was inappropriate since the plant is heterozygous both for stature and for bud coloration. Also, as determined by Cleland (1924), the chromosome configuration of the plant proved to be a circle of 12 and one pair in contrast to the 7 pairs of *franciscana*. It seems best to make this correction in nomenclature rather than to let the matter drift especially since I have a legitimate *franciscana sulfurea* in cultivation and the character *sulfurea* is one that seems likely to be of further interest in *Oenothera* genetics. The matter will receive further consideration in the section headed Type F. Sulfur, Tall, Green Buds; *ssD \widehat{G} g \widehat{g}* .

The true *franciscana sulfurea*, *ssDDgg*, has appeared a number of times from various crosses. The plant is similar to *franciscana* in height, foliage and bud coloration, differing only in its sulfur flowers, which come to bloom two weeks later than do those of *franciscana*. Its pollen, as in *franciscana*, is perfect and its seed fertility of about 90 per cent is equally good. My line in cultivation has the history given in Table 4. It started from a cross *franciscana* \times type F, *SSDDgg* \times *ssD \widehat{G} g \widehat{g}* (sulfur, tall, green buds). Since pollen carrying the genes *DG* fails to mature, this cross gives a

TABLE 4
TYPE B THE LINE OF TRUE *franciscana sulcata*, SULFUR, TALL, RED BUDS, *ssDDgg*

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
A × F 23 30	<i>SSDDgg</i> × <i>ssDDgg</i> 20 21-5 × 20 23-6				Culture partially grown, 48 yellow tall red, <i>ssDDgg</i>	
F ₂ A × F 24-59a	<i>ssDDgg</i> yellow tall red 23 30-5	263	247	93.9	185 yellow tall red 19 yellow dwarf red 32 sulfur tall red 1 sulfur dwarf red <hr/> 237	10
Type B 280 Emerson	<i>ssDDgg</i> sulfur tall red 24-59a-5	150	143	95.3	140 sulfur tall red 2 smaller plants 1 rosette	
Type B 546 Emerson	<i>ssDDgg</i> 280-21	100 Earth sown	59		59 sulfur tall red	
Type B 29.62	<i>ssDDgg</i> 546-1	484 (1 capsule)	440	90.9	434 sulfur tall red 1 narrow-leaved dwarf rosette	5
Type B 30.62	<i>ssDDgg</i> 29 62-151	299 (1 capsule)	247	82.6	246 sulfur tall red	1

uniform F_1 generation, $SsDdgg$, plants heterozygous for flower color and for stature but homozygous for red bud color. The F_2 generation, as would be expected, segregates yellow tall, yellow dwarf, sulfur tall and sulfur dwarf, but the sulfur tall and all dwarf plants are below numerical expectations. The sulfur tall plants would be expected in the ratio of $1 ssDDgg : 2 ssDdgg$. In the history of this line, Table 4, a selection among the sulfur tall in the F_2 culture 24 59a gave to Emerson (1931) culture 280 followed by culture 546 again through the selection of a tall plant. This seems to have established the homozygous type since no dwarfs appeared in later large generations and its breeding behavior has been that of a homozygote. An interesting origin of the true *franciscana sulfurea* through an unusual number of crossovers from a plant of type F will be discussed in the section of the paper entitled Crossovers from data given in Table 11, culture 26 76.

The true *franciscana sulfurea* of my line, tested in 1933, has 7 pairs of chromosomes. This configuration first became known from studies of Cleland (1928) and of Illick (1929), both on material from Shull's garden. Dr Shull has kindly sent me the pedigree background out of which came his line of *franciscana sulfurea*. The history is too complicated to give in full but the following summary is pertinent. It started with a sulfur tall red plant, 18115(15), from a cross yellow tall red \times sulfur tall green, the two parents being segregates from the double reciprocal $(F \times A) \times (A \times F)$, Shull's culture 17207. The sulfur tall red plant, 18115(15), was pollinated by a yellow tall red, 18185(66), derived from a cross of form F by a green budded *nanella*. In the progeny was a yellow tall red, 19203(11), heterozygous for yellow since it threw a sulfur tall red, 20258(122). This plant was the beginning of Shull's line of true *franciscana sulfurea*.

Bearing on the cytology of *franciscana sulfurea* are studies of Emerson's (1931a, p. 332) who determined the chromosome configurations of 11 plants with red buds ($SsDdgg$) from the F_1 of *franciscana* \times type F, $SSDDgg \times ssDdgg$. Ten of

these plants had 7 pairs and one a circle of 4 and 5 pairs. The plants with 7 pairs indicate that the set of chromosomes carrying *sdg* must be homologous to the set carrying *SDg* and that the plant with a circle of 4 and 5 pairs must have resulted from a segmental interchange. In the F_2 from the plant (58-1) with a circle of 4 chromosomes and 5 pairs Emerson tested three plants two of which showed the same configuration while the third had 7 pairs, results which would be expected since all of the gametes are fertile with one another.

TYPE C. YELLOW, DWARF, RED BUDS, *O. franciscana*
nana: *SSddgg*; TABLE 5

The dwarf, *franciscana nana*, has arisen frequently from appropriate crosses. The plant, 5 dm. high, grows to about one half the height of *franciscana* and has leaves somewhat narrower and flowers not quite so large; the rosette leaves turn red very early. It is not a small dwarf, but nevertheless is readily distinguished from its tall relative. As with *franciscana* the pollen is perfectly formed, but the seed fertility, from 60 to 80 per cent, is not so high.

The pedigree of my line in cultivation is given in Table 5. It started with the same cross *franciscana* \times type F, *SSDDgg* \times *ssD \widehat{G} dg*, as that which gave the true *franciscana sulfurea*, Table 4. From the F_1 of this cross yellow dwarf reds may be obtained at once as shown in culture 24 59a of Table 4, but the line followed a different history. An F_1 plant, *SsDdg*, furnished the pollen for a back cross to the parent type F, *ssD \widehat{G} dg*, giving the culture 24 64b, $F \times (A \times F)$, of Table 5. Since *DG* is not lethal in the egg the progeny of this back cross will consist of six combinations which actually appeared as listed for this culture. Yellow dwarf reds were represented by only 4 plants whereas in a regular segregation they should have made one eighth of the total culture. The line was continued through a selfed plant of yellow tall green buds, type E of the series. This plant was *SsD \widehat{G} dg* because the next generation gave yellow dwarf reds in abundance, and a

TABLE 5
TYPE C THE LINE OF *franciscana nana*, YELLOW, DWARF, RED BUDS, *SSdgg*

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
A × F 23 30	<i>SSDdgg</i> × <i>SSDgGg</i> 20 21-5 × 20 23-6				Culture partially grown, 48 yellow tall red, <i>SSdgg</i>	
F × (A × F) 24-64b	<i>SSDgGg</i> × <i>SSdgg</i> 23 23-6 × 23 30-5	273 (1 capsule)	216	79.1	124 yellow tall green 20 yellow tall red 4 yellow dwarf red 40 sulfur tall green 16 sulfur tall red 1 sulfur dwarf red 205	11
Type E 26 75	<i>SSDgGg</i> yellow tall green 24 64b-4	270 (1 capsule)	192	71.1	76 yellow tall green 4 yellow tall red (crossovers, pollen 50 per cent bad) 96 yellow dwarf red 1 yellow dwarf green (crossover, pollen 50 per cent bad) 5 sulfur dwarf red 182	10
Type C 27 63	<i>SSdgg</i> yellow dwarf red 26 75-1	335 (1 capsule)	231	68.9	226 yellow dwarf red 1 narrow-leaved rosette	4
Type C 28 63	<i>SSdgg</i> 27 63-93	428 (1 capsule)	248	57.9	241 yellow dwarf red	7
Type C 29 63	<i>SSdgg</i> 28 63-173	337 (1 capsule)	206	61.1	179 yellow dwarf red	27
Type C 30 63	<i>SSdgg</i> 29 63-65	395 (1 capsule)	311	78.7	302 yellow dwarf red	9

few sulfur dwarf reds, culture 26 75, Table 5. There were 96 yellow dwarf reds and these constituted more than half of the culture, expectations calling for a proportion of three eighths. Interesting features of this culture were the 4 cross-overs, yellow tall red balanced by one individual of yellow dwarf green, a weak plant failing to set seed, which was the first representative recognized of type G. From this round-about history arose the particular plant of yellow dwarf red (26.75-1) out of which came the series of large cultures, Table 5, that established the line of *franciscana nana*, SSddgg.

Studies of meiosis in *franciscana nana* from selected parent plants of my line in 1928 and 1933 showed the chromosome configuration to be 7 pairs

TYPE D SULFUR, DWARF, RED BUDS, *O franciscana sulfurea nana*; ssddgg, TABLE 6

This type recessive for the characters under consideration is readily obtained in large cultures from suitable hybrids, but the numbers are generally far below expectations. The plant is about 5 dm. high, half as tall as *franciscana sulfurea*, with leaves smaller and narrower and with smaller flowers. Its vegetative characters are quite the same as those of *franciscana nana* from which it differs in having sulfur flowers and rosette leaves that do not turn red early. The pollen is perfectly formed as in the other types, A, B, and C, but like *franciscana nana* the seed fertility, Table 6, is not so high as in *franciscana*.

The easiest way to obtain sulfur dwarf red is to grow large cultures from all viable seeds of type F, sulfur tall green, ssDGg. Since DG is lethal in the pollen of type F this plant reproduces itself and throws sulfur dwarf red. Type F was carried from the original plant (14 56w) through three generations of small incomplete cultures, Table 8, before obtaining the dwarf. Then a large culture (23 23, Table 8) from seed of type F, forced to complete germination, gave a segregation of 300 sulfur tall green and 181 sulfur dwarf red and the situation became clear. The cultivated line of

TABLE 6
 TYPE D THE LINE OF *franciscana sulfurea nana*, SULFUR, DWARF, RED BUDS, *ssidgg*

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
Type F 24.23	<i>ssidgg</i> sulfur tall green 23 23-6	265 (1 capsule)	194	73 2	Culture partially grown, 16 sulfur tall green, 9 sulfur dwarf red	
Type D 26 24	<i>ssidgg</i> sulfur dwarf red 24.23-1	456 (1 capsule)	264	57 9	Culture partially grown, 63 sulfur dwarf red	
Type D 27 24	<i>ssidgg</i> sulfur dwarf red 26 24-37	290 (1 capsule)	218	75 2	215 sulfur dwarf red	3
Type D 28 64	<i>ssidgg</i> 27 24-11	182 (1 capsule)	128	70 3	127 sulfur dwarf red	1
Type D 29.64	<i>ssidgg</i> 28.64-122	211 (1 capsule)	186	88 1	183 sulfur dwarf red	3
Type D 30.64	<i>ssidgg</i> 29 64-57	175 (1 capsule)	140	80	137 sulfur dwarf red	3

franciscana sulfurea nana started with culture 26.24, Table 6, and the line bred wholly true through four later generations of considerable numbers.

Emerson (1928) reported 7 pairs of chromosomes during meiosis in *franciscana sulfurea nana*, conditions which I confirmed in the parent plant of my line in 1933. The plant, therefore, agrees in chromosome configuration with *franciscana*, the true *franciscana sulfurea* and *franciscana nana*, all four types being homozygous

TYPE E YELLOW, TALL, GREEN BUDS, d^h*franciscana* . *sulfurens*; $Ss\widehat{DG}\widehat{dg}$, TABLE 7

This interesting form has the yellow flowers and the height of *franciscana* but the buds are green. Since the linked genes \widehat{DG} are always associated with a pollen lethal the \widehat{DG} group cannot be inherited through the pollen. Pollen is somewhat less than 50 per cent perfect. Seed fertility around 70 per cent is only fair.

The pedigree of type E is given in Table 7. The first plant was a segregate from the back across $F \times (A \times F)$ $A \times F$, $SSDdgg \times ss\widehat{DG}\widehat{dg}$, gives only one type, $SsDdgg$, because \widehat{DG} is pollen lethal. Therefore, $F \times (A \times F)$ is $ss\widehat{DG}\widehat{dg} \times SsDdgg$ and should give a progeny, if fully represented, in the proportions of 2 yellow tall greens, 1 yellow tall red, 1 yellow dwarf red, 2 sulfur tall greens, 1 sulfur tall red, and 1 sulfur dwarf red. These classes were represented in culture 24.64b, Table 7, but the numbers showed small proportions of sulfurs, dwarfs and reds.

The yellow tall greens of this culture, 24.64b, from $F \times (A \times F)$ in theory might have been either $Ss\widehat{DG}\widehat{dg}$ or $Ss\widehat{DG}\widehat{dg}$, but the plant selected, type E, was heterozygous for stature, $Ss\widehat{DG}\widehat{dg}$, since it threw dwarfs in culture 26.75. A complete segregation in this culture would have called for 3 yellow tall greens, 3 yellow dwarf reds, 1 sulfur tall green, and 1 sulfur dwarf red, but there were no sulfur tall greens and very few sulfur dwarf reds. The yellow tall greens again might in theory have been homozygous for yellow in the

TABLE 7
TYPE E. THE LINE OF YELLOW, TALL, GREEN BUDS, $S_1\widehat{D}Gd\widehat{g}$

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
A × F 23 30	$SSDDgg \times S_1\widehat{D}Gd\widehat{g}$ 20 21-5 × 20 23-6				Culture partially grown, 48 yellow tall red, S_1Ddgg	
F × (A × F) 24 64b	$S_1\widehat{D}Gd\widehat{g} \times S_1Ddgg$ 23 21-5 × 20 23-6	273 (1 capsule)	216	79.1	124 yellow tall green 20 yellow tall red 4 yellow dwarf red 40 sulfur tall green 16 sulfur tall red <u>1</u> sulfur dwarf red 205	11
Type E 26 75	$S_1\widehat{D}Gd\widehat{g}$ yellow tall green 24 64b-4	270 (1 capsule)	192	71.1	76 yellow tall green 4 yellow tall red (crossovers, pollen 50 per cent bad) 96 yellow dwarf red 1 yellow dwarf green (crossover, pollen 50 per cent bad) <u>5</u> sulfur dwarf red 182	10

TABLE 7—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
Type E 27 64	$Sr\widehat{D}Gd\widehat{g}$ 26 75-9	430 (2 capsules)	326	75 8	128 yellow tall green 3 yellow tall red (crossovers, pollen 50 per cent bad) 172 yellow dwarf red 10 yellow dwarf green (crossovers, pollen 50 per cent bad) <u>313</u>	13
Type E 28 65	$Sr\widehat{D}Gd\widehat{g}$ 27 64-88	391 (1 capsule)	357	91 3	157 yellow tall green 1 yellow tall red (crossover, pollen 50 per cent bad) 189 yellow dwarf red <u>347</u>	10
Type E 29 65	$Sr\widehat{D}Gd\widehat{g}$ 28 65-29	493 (2 capsules)	345	69 9	122 yellow tall green 1 triploid, yellow tall green 209 yellow dwarf red 2 rosettes <u>334</u>	11
Type E 30.65	$Sr\widehat{D}Gd\widehat{g}$ 29.65-162	103 (1 capsule)	71	68 9	27 yellow tall green 39 yellow dwarf red 66	5

proportions of 1 : 2, and the four later generations of the line produced no sulfur-flowered plants. This suggested a selection of parent plants homozygous for yellow but there is the following evidence that through this period (1927-1930) the line had continued heterozygous for yellow, $Ss\widehat{DG}\widehat{dg}$.

The cross $E \times F$, type E being parent plants in the line from cultures 28 65 and 29 65, Table 7, gave sulfur flowered forms and since type F is homozygous for sulfur it follows that type E must have been heterozygous. This cross was then $Ss\widehat{DG}\widehat{dg} \times ss\widehat{DG}\widehat{dg}$ and since \widehat{DG} is not carried by fertile pollen the cross might be expected to give in equal proportions yellow tall greens, yellow dwarf reds, sulfur tall greens and sulfur dwarf reds. All of these segregates were present but in numbers far from uniform. As shown in Table 9, cultures 29 39 and 30 44, sulfur tall greens appeared in good numbers and there were a few sulfur dwarf reds. Yellow dwarf reds made up more than half of the cultures while the few yellow tall greens were more scarce than the sulfur dwarf reds. Progenies from the same cross involving parents of a later date were grown in 1931, Table 18, and gave a similar segregation of sulfur tall greens and sulfur dwarf reds. For the matter under consideration the evidence is clear that the line at this time, 1928-1930, was heterozygous for yellow.

The reciprocal cross $F \times E$, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{dg}$, again might be expected to give in equal proportions the same segregates, yellow tall greens, yellow dwarf reds, sulfur tall greens and sulfur dwarf reds. The progenies of the two cultures 29.40 and 30 45, Table 9, were, however, wholly yellow tall greens and yellow dwarf reds except for one plant of sulfur dwarf red (30 45) and a crossover yellow dwarf green; Table 18 also shows the same scarcity of sulfur dwarf reds and the absence of sulfur tall greens. It should be noted that the seed germination in these cultures was very low. The presence of the few sulfur dwarf reds proved that type E was heterozygous for yellow.

The departures from the expected ratios in the progeny of the two crosses $E \times F$ and $F \times E$ present problems that will

be discussed in a later section of the paper. There is the possibility of competition within the ovule between megaspores and between developing female gametophytes carrying different complexes (Renner, 1921), the possibility of selective fertilization, the possibility of different rates of pollen tube growth. We shall see later that these irregularities are not wholly accounted for by hypotheses of differential pollen tube growth.

The chromosome configuration in type E, determined from plants of the line in 1928 and 1934, is a circle of 12 and one pair, the same configuration as in type F. Alternate chromosomes usually go to the same pole of the spindle. The following counts of complete groups of chromosomes indicate how infrequent are irregularities of chromosome distribution during meiosis: normal anaphases of first division 67, normal interkineses 94, normal anaphases of second division 53, non-disjunctions (6 and 8) 21, lagging chromosomes 2. The proportion of irregularities in this examination was 9.7 per cent.

The 50 per cent and more of empty and shriveled pollen grains found in types E, F, G and H is associated with the dominant gene for green buds, which means that this pollen abortion is always present in green budded plants and never in plants with red buds except for certain crossovers. It then becomes a matter of interest to know whether or not the *DG* group is eliminated by way of the empty pollen grains. The perfect pollen in type E, as in *franciscana*, apparently contains only one type of starch grain, very small and spindle-shaped. The grains germinate readily in a moist chamber in smears on slides from the secretions of their own stigma and equally well in the stigma secretions of type F and type A (*franciscana*), and data on this germination are given below.

	Full grains germinating	Full grains failing to germinate	Per cent germination	Empty and shriveled grains
Pollen E in secretion E	84	97	46.4	260
Pollen E in secretion F	20	24	45.4	69
Pollen E in secretion A	81	99	45.0	211
Totals	185	220	45.7	540

It is true that in the tests only 46.4 per cent of the full grains germinated in the secretions from their own stigma which might suggest the presence of a lethal in 50 per cent of the full grains, but pollen of *franciscana* gave a percentage of only 64.3 in its own secretion and there are no reasons to suspect pollen lethals in that plant. Also, the full pollen of type F, which presents the same degree of pollen sterility, gave in similar tests a germination percentage of 70.3. It is probably difficult to spread pollen so that all of it becomes sufficiently wet with the smeared secretions to germinate, and the tests probably did not secure a full expression of its viability. The number of full grains counted in the fields of these examinations was 405 (185 + 220) compared with 540 empty and shriveled grains, the bad pollen thus constituting 57.1 per cent of the smears. This is a percentage apparently high enough to include a possible 50 per cent sterility due to a lethal plus abortive pollen resulting from irregularities in meiosis. From the evidence so far developed I am inclined to hold the hypothesis that the \overline{DG} group with its associated pollen lethal is segregated in the pollen grains that become empty and shriveled.

TYPE F. SULFUR, TALL, GREEN BUDS, s d^hfranciscana sulfurens, ss $\overline{DG}\overline{d}g$, TABLE 8

This plant through a misnomer (Davis, 1916, p. 243) has been discussed in the *Oenothera* literature under the name "*franciscana sulfurea*" which it is not because green buds are not found in races of *Oenothera franciscana*. The true *franciscana sulfurea* is type B of this paper with the formula ssDDgg. Type F has the height of *franciscana* but the flowers are sulfur and the buds green. The pollen is somewhat less than 50 per cent perfect, seed fertility is frequently above 80 per cent. As in type E the \overline{DG} group is not inherited through the pollen.

Type F has arisen only once (plant 14.56w, Table 8) and then in the F₃ of a cross *biennis* × *franciscana* (culture 14.56). The gene for green buds with the associated pollen lethal presumably came from the *biennis* parent as did also the gene

TABLE 8
TYPE F THE LINE OF SULFUR, TALL, GREEN BUDS, *SDGdg*

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
13 36	<i>biennis</i> × <i>franciscana</i>	Earth sown			Culture partially grown, 150 plants, uniform, strongly patrocimic, yellow tall red buds	
14 56	yellow tall red 13 36a	Earth sown			Culture partially grown, 50 yellow tall red 1 sulfur tall green (14-56w)	
16 23	sulfur tall green 14-56w	220 (1 capsule)	188	85.4	Culture partially grown, 64 sulfur tall green	
17 23	sulfur tall green 16 23a	Earth sown			Culture partially grown, 12 sulfur tall green	
20 23	sulfur tall green 17-23 1-3	Earth sown			Culture partially grown, 25 sulfur tall green	
21 23	sulfur tall green 20 23-6	403 (1 capsule)	354	87.8	Culture partially grown, 21 sulfur tall green 2 sulfur dwarf red	
Type F 23 23	<i>SDGdg</i> 21 23-9	879 (3 capsules)	673	76.6	300 sulfur tall green 181 sulfur dwarf red	192

TABLE 8—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Dead
Type F 24.23	$ss\overline{D}\overline{G}\overline{d}g$ 23 23-6	265 (1 capsule)	194	73.2	Culture partially grown, 16 sulfur tall green 9 sulfur dwarf red	
Type F 26.23	$ss\overline{D}\overline{G}\overline{d}g$ 24 23-2	Earth sown			Culture partially grown, 11 sulfur tall green 4 sulfur dwarf red	
Type F 27.23	$ss\overline{D}\overline{G}\overline{d}g$ 26 23-5	350 (1 capsule)	329	94	207 sulfur tall green 117 sulfur dwarf red	5
Type F 28.66	$ss\overline{D}\overline{G}\overline{d}g$ 27 23-141	301 (1 capsule)	254	84.4	124 sulfur tall green including one triploid 119 sulfur dwarf red	11
Type F 29.66	$ss\overline{D}\overline{G}\overline{d}g$ 28 66-120	617 (2 capsules)	92	14.9	26 sulfur tall green 55 sulfur dwarf red 1 narrow leaved dwarf	10
Type F 30.66	$ss\overline{D}\overline{G}\overline{d}g$ 29.66-80	353 (1 capsule)	264	74.8	99 sulfur tall green including one triploid 162 sulfur dwarf red	3

for sulfur The plant first appeared in my garden of 1914 and at that time it was not known that green buds in this material were allelomorphic to and dominant over red buds Also, the line from the first plant of type F (14 56w) was carried along for three generations in partially grown cultures (Table 8, cultures 16.23, 17.23, 20 23) before it was discovered to be heterozygous for height and bud color

The first culture (23 23, Table 8) in which all plants were set in the field was grown in 1923 It gave 300 plants, sulfur tall green, and 181 plants, sulfur dwarf red, but the very high mortality in this culture made the ratio uncertain. Later generations fully grown and with small mortality as shown in Table 8 (cultures 27 23, 28 66, 29 66 and 30.66) gave higher proportions of sulfur dwarf red, the combined numbers for these cultures being 456 sulfur tall greens and 453 sulfur dwarf reds The formula for the plant thus became established as $ss\widehat{D}\widehat{G}\widehat{d}g$

The cytology of type F was thoroughly studied by Cleland (1924) from material out of my garden of 1920 and before it was known that the plant was heterozygous for height and bud coloration He therefore used the name "*franciscana sulfurea*" Cleland found the chromosome configuration to be a circle of 12 and one pair and these observations were confirmed by Emerson (1928) in material from later generations of the same line I found the line to have this chromosome configuration in 1935: Cleland recorded for 623 cells in interkinesis a proportion of irregularities from non-disjunction (6 and 8) amounting to 16 per cent.

The perfect pollen contains only one kind of starch grain, very small and spindle shaped, as in type F and in *franciscana* There is given below data on the germination of full pollen

	Full grains germinating	Full grains failing to germinate	Per cent germination	Empty and shriveled grains
Pollen F in secretion F	90	38	70.3	16.7
Pollen F in secretion E	102	34	75	17.2
Pollen F in secretion A	55	35	61.5	9.3
Totals	247	107	69.7	43.2

TABLE 9
 RECIPROCAL CROSSES, TYPES E × F AND F × E, ESTABLISHING THE FORMULA $Sr\widehat{DGd\widehat{g}}$ FOR TYPE E

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
E × F 29.39	$Sr\widehat{DGd\widehat{g}} \times sr\widehat{DGd\widehat{g}}$ 28 65-29 × 28 66-120	364 (1 capsule)	326	89.6	3 yellow tall green, including one triploid 155 yellow dwarf red 49 sulfur tall green 10 sulfur dwarf red 4 yellow tall red (crossovers, pollen 50 per cent bad) 4 yellow dwarf green (crossovers, pollen 50 per cent bad) 1 sulfur dwarf green (crossover, pollen 50 per cent bad) <hr/> 226	100 (95 as seedlings)
F × E 29.40	$sr\widehat{DGd\widehat{g}} \times Sr\widehat{DGd\widehat{g}}$ 28 66-120 × 28 65-29	490 (2 capsules)	106	21.6	28 yellow tall green 63 yellow dwarf red 1 yellow dwarf green (crossover, pollen 50 per cent bad) <hr/> 92	14 (11 as seedlings)

TABLE 9—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Dead
E × F 3044	$S_1 D G d_1 \times S_1 D G d_1$ 29 65-162 × 29 66-80	476 (2 capsules)	235	49.4	9 yellow tall green, including 3 triploids 121 yellow dwarf red 93 sulfur tall green 5 sulfur dwarf red 1 yellow tall red (crossover, pollen 50 per cent bad) 1 sulfur dwarf green (crossover, pollen 50 per cent bad) <hr/> 230	5 (4 as seedlings)
F × E 3045	$S_1 D G d_1 \times S_1 D G d_1$ 29 66-80 × 29 65-162	954 (3 capsules)	409	42.9	74 yellow tall green 206 yellow dwarf red 1 sulfur dwarf red <hr/> 281	128 (127 as seedlings)

grains in smears of their own stigma secretions and in the secretions of type E and type A (*franciscana*)

The total number of full grains counted in the fields of these examinations was 354 (247 + 107) compared with 432 empty and shriveled grains, the bad pollen constituting 54.9 per cent of the smears. The percentages of germination among the full pollen grains is too high to suggest the presence of a lethal that might render inactive 50 per cent of the full grains and it seems more likely that the DG group with its associated lethal is eliminated through the shriveled and empty pollen grains.

TYPE G YELLOW, DWARF, GREEN BUDS $d^{hfranciscana} d^{sulfurens} Ssd\widehat{Gd}g$, TABLE 10

In the course of the studies occasional plants of certain origins were noted which had yellow flowers, dwarf stature, and green buds. They were plants much less vigorous than the red budded dwarfs *franciscana nana* and *franciscana sulfurea nana*, and their pollen was less than 50 per cent good. It became clear from their breeding that the gene for green buds was here also linked with a pollen lethal as in types E and F.

As listed in Table 10 yellow dwarf greens may arise as crossovers in cultures of type E (cultures 26.75, 27.64), but they have never carried themselves far in selfed lines, always disappearing after the first or second generation. They have also appeared as crossovers from reciprocal crosses between types E and F (cultures 29.39, 29.40) where they did not reproduce themselves when selfed (cultures 30.46, 30.47). There has therefore been no line of yellow dwarf greens beyond a second generation. Progenies from selfed yellow dwarf greens were yellow dwarf reds except for 5 sulfur dwarf reds (28.73, 30.47) and the 4 yellow dwarf greens appearing in certain first generations (28.67, 28.72).

The breeding behavior of yellow dwarf green shows the plant to have been heterozygous for flower color and for bud color, the formula being $Ssd\widehat{Gd}g$. With the expression of G

TABLE 10
TYPE G LINES OF YELLOW, DWARF, GREEN BUDS, $S_{11}D_{11}G_{11}$

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
Type E 26 75	$S_{11}D_{11}G_{11}$ yellow tall green 24-64b-4	270 (1 capsule)	192	71 1	Complete list given in Table 7 1 yellow dwarf green (26 75-118, crossover, pollen 50 per cent bad) Attempts to self-pollinate failed	10
27 65	yellow dwarf green, open pollinated 26 75-118	384 (1 capsule)	352	91 6	103 yellow tall green 210 yellow dwarf red 4 yellow dwarf green 29 sulfur tall green <hr/> 346	6
Type G 28 67	$S_{11}D_{11}G_{11}$ 27 65-304	367 (1 capsule)	232	63 2	217 yellow dwarf red 1 yellow dwarf green <hr/> 218	14
Type E 27 64	$S_{11}D_{11}G_{11}$ yellow tall green 26 75-9	430 (2 capsules)	326	75 8	Complete list given in Table 7 10 yellow dwarf green (crossovers, pol- len 50 per cent bad)	11
Type G 28 72 %	$S_{11}D_{11}G_{11}$ 27 64-301	249 (1 capsule)	164	65 9	157 yellow dwarf red 3 yellow dwarf green <hr/> 160	4

TABLE 10—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
Type G 28 73	$S_{11}dGd\widehat{g}$ 27 64-306	198 (2 capsules)	119	60.1	98 yellow dwarf red 1 sulfur dwarf red 7 failed to mature 106	13
Type G 28 74	$S_{11}dGd\widehat{g}$ 27 64-42	253 (1 capsule)	168	66.4	131 yellow dwarf red 6 failed to mature 137	31
E × F 29 39	$S_{11}dGd\widehat{g} \times S_{11}dGd\widehat{g}$ 28 65-29 × 28 66-120	364 (1 capsule)	326	89.6	Complete list given in Table 9 4 yellow dwarf green (crossovers, pollen 50 per cent bad)	100 (95 as seedlings)
Type G 30 47	$S_{11}dGd\widehat{g}$ 29 39-178	192 (1 capsule)	120	62.5	103 yellow dwarf red 4 sulfur dwarf red	13
F × E 29 40	$S_{11}dGd\widehat{g} \times S_{11}dGd\widehat{g}$ 28 66-120 × 28 65-29	490 (2 capsules)	106	21.6	Complete list given in Table 9 1 yellow dwarf green (29 40-14, crossover, pollen 50 per cent bad)	14
Type G 30 46	$S_{11}dGd\widehat{g}$ 29 40-14	242 (1 capsule)	91	37.6	84 yellow dwarf red 3 failed to mature	4

through the pollen eliminated by its linked lethal the results of perfect segregation from such plants, $Ss\bar{a}\bar{G}\bar{a}g$, would be 3 yellow dwarf greens, 3 yellow dwarf reds, 1 sulfur dwarf green and 1 sulfur dwarf red. Yellow dwarf greens following selfings (28 67, 28 72) were represented by 4 plants against the total of 790 yellow dwarf red segregates where expectations assuming an expression of complete segregation would be a ratio of 1 : 1. Sulfur dwarf reds were represented by 5 plants against the 790 yellow dwarf reds where complete segregation called for a ratio of 1 : 3. Sulfur dwarf greens did not appear at all.

The percentages of seed germination (generally above 60 per cent) offer no help towards an explanation of the absence of sulfur dwarf greens and the scarcity of yellow dwarf greens and sulfur dwarf reds from cultures of yellow dwarf green. We are left with the possibilities of a differential rate of growth between pollen tubes Sdg and sdg , of selective competition among the megaspores SdG , Sdg , sdG and sdg or among their gametophytes, of preferential fertilization, of selective competition among the possible types of zygotes and embryos. The material presents difficult problems, the more so because it is physiologically weak.

Plants of yellow dwarf green produced so few flowers that cytological studies were not attempted. From its breeding behavior the type may be expected to have the chromosome configuration of types E and F, a circle of 12 and 1 pair.

TYPE H SULFUR, DWARF, GREEN BUDS, $s d^{hfranciscana} d sulfurens, ss\bar{a}\bar{G}\bar{a}g$, TABLE 11

This plant has appeared even less frequently than type G and like it is physiologically weak, difficult to self and to grow. It has arisen through crossovers, Table 11, directly from type F (culture 26.76) and from the cross $E \times F$ (cultures 29.39, 30.44). It might be expected through crossovers from type E and from $F \times E$, but it has not appeared. As would be expected from the presence of G its pollen is less than 50 per cent good. It reproduces itself

TABLE II
TYPE H LINES OF SULFUR, DWARF, GREEN BUDS, $ssd\widehat{Gd}g$

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Dead
Type F 26 76	$ss\widehat{D}Gd\widehat{g}$ sulfur tall green 24.64b-7 from $F \times (A \times F)$, Table 7	221 (1 capsule)	203	91.9	105 sulfur tall green 35 sulfur dwarf red 30 sulfur tall red (crossovers, pollen perfect) 5 sulfur tall red, triploids 9 sulfur dwarf green (crossovers, pollen 50 per cent bad) 5 rosettes <u>189</u>	14
Type H 27 66	$ssd\widehat{Gd}g$ 26 76-189	235 (6 small capsules)	20	8.5	11 sulfur dwarf red, including one triploid 3 sulfur dwarf green 3 failed to mature <u>17</u>	3

TABLE 11—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Dead
Type H 28 68	$sdGd\bar{g}$ 27 66-8	137 (5 capsules)	47	34.3	40 sulfur dwarf red 1 sulfur dwarf green	6
Type H 28 69	$sdGd\bar{g}$ 27 66-18	230 (2 capsules)	119	51.9	119 sulfur dwarf red	
E × F 29.39	$S_1D\bar{G}d\bar{g} \times s_1D\bar{G}d\bar{g}$ 28 65-29 × 28 66-120	364 (1 capsule)	326	89.6	Complete list given in Table 9 1 sulfur dwarf green (29 39-202, crossover, pollen 50 per cent bad)	100 (95 as seedlings)
Type H 30.48	$sdGd\bar{g}$ 29 39-202	34 (1 capsule)	18	52.9	16 sulfur dwarf red	2
E × F 30.44	$S_1D\bar{G}d\bar{g} \times s_1D\bar{G}d\bar{g}$ 29 65-162 × 29 66-80	467 (2 capsules)	235	49.4	Complete list given in Table 9 1 sulfur dwarf green (30.44-66, crossover, pollen 50 per cent bad)	5
Type H 31.48	$sdGd\bar{g}$ 30.44-66	533 (6 capsules)	206	38.6	178 sulfur dwarf red	28

rarely when selfed and has never continued beyond the second generation in the lines cultivated.

The first plants noted of sulfur dwarf green appeared in a culture from a plant of type F, *ssDĠgġ*, remarkable for the large number of crossovers, 30 plants of sulfur tall red and 9 plants of sulfur dwarf green (Table 11, culture 26.76) This plant of type F was not from the line in cultivation, Table 8, which has never by a crossover thrown sulfur dwarf green, but it was a segregate from the cross $F \times (A \times F)$, *ssDĠgġ* \times *SsDdgg* (Table 7, culture 24.64b) The plants F and A involved in this cross were, however, out of the lines in cultivation There is, therefore, the fact of a sudden appearance of numerous crossovers from type F selfed following its reconstruction as a segregate from the cross $F \times (A \times F)$

Plants of sulfur dwarf green from crossovers out of the cross $E \times F$ have appeared twice (cultures 29.39 and 30.44), in each case represented by a single plant The parent plants of the crosses were out of the cultivated lines

Sulfur dwarf green selfed gives progenies almost wholly of sulfur dwarf red. As set down in Table 11 there were five such cultures grown (27.66, 28.68, 28.69, 30.48, 31.48) and only two of these reproduced sulfur dwarf green, a total of 4 plants in contrast with a total of 362 sulfur dwarf reds, assuming an expression of complete segregation the ratio should have been 1 : 1 The seed fertility of sulfur dwarf green, low as it is, cannot account for the scarcity of the form as a segregate in contrast to sulfur dwarf red Other factors must be operative to cut down the numbers with the possibilities of competition between the two types of megaspores or their gametophytes Since there is only one type of pollen grain to function (*sdg*) there is at least no factor of differential pollen tube growth to be considered.

Type H, as with type G, produced so few flowers that no attempt was made to establish its chromosome configuration which, however, is probably a circle of 12 and 1 pair, as in types E and F.

TABLE 12
MONOHYBRIDS INVOLVING THE HOMOZYGOUS TYPES A, B, C, D

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Died
B × A 29 31	<i>ssDDgg</i> × <i>SSDDgg</i> 546-1 × 28 61-626	336 (1 capsule)	296	88 1	287 yellow tall red, <i>SsDDgg</i> 2 rosettes	7
A × B 29 32	<i>SSDDgg</i> × <i>ssDDgg</i> 28 61-626 × 546-1	269 (1 capsule)	205	76 1	191 yellow tall red, <i>SsDDgg</i>	14
C × A 29 33	<i>SSddgg</i> × <i>SSDDgg</i> 28 63-173 × 28 61-626	288 (2 small capsules)	251	87 1	241 yellow tall red, <i>SSDdgg</i>	10
A × C 29 34	<i>SSDDgg</i> × <i>SSddgg</i> 28 61-626 × 28 63-173	469 (1 capsule)	266	56 7	259 yellow tall red, <i>SSDdgg</i> 1 rosette	6
D × B 29 35	<i>ssddgg</i> × <i>ssDDgg</i> 28 64-122 × 546-1	136 (3 small capsules)	30	21 3	24 sulfur tall red, <i>ssDdgg</i>	6
B × D 29 36	<i>ssDDgg</i> × <i>ssddgg</i> 546-1 × 28 64-122	240 (1 capsule)	174	72 5	157 sulfur tall red, <i>ssDdgg</i>	17
D × C 29 37	<i>ssddgg</i> × <i>SSddgg</i> 28 64-122 × 28 63-173	192 (1 capsule)	93	48.4	87 yellow dwarf red, <i>Ssddgg</i>	6
C × D 29 38	<i>SSddgg</i> × <i>ssddgg</i> 28 63-173 × 28 64-122	288 (1 capsule)	224	77 8	203 yellow dwarf red, <i>Ssddgg</i>	21

MONOHYBRIDS INVOLVING THE HOMOZYGOUS TYPES
A, B, C, D TABLE 12

A full set of monohybrids was grown involving the four homozygous types: A, *franciscana*; B, the true *franciscana sulfurea*, C, *franciscana nana*, D, *franciscana sulfurea nana*. The pertinent data are given in Table 12. The cultures were large and established the dominance of yellow over sulfur and tall over dwarf. The pollen of the hybrids was perfect. The percentages of seed germination were irregular, and when type D was the female parent the percentages were markedly low.

SEGREGATION IN THE F_2 GENERATIONS FROM THE MONO-
HYBRIDS INVOLVING THE HOMOZYGOUS TYPES A, B,
C, D. STYLE-CUTTING EXPERIMENTS COMPARED
WITH FULL TIME FOR POLLEN TUBE
GROWTH TABLE 13

Table 13 gives data on the F_2 generations from all possible monohybrids involving the homozygous types A, B, C, D. Those that will segregate yellow and sulfur are *SsDDgg* from $B \times A$ and $A \times B$ (cultures 30 71, 30 72, 30 73, 30 74), and *Ssddgg* from $D \times C$ and $C \times D$ (cultures 30 83, 30 84, 30 85, 30 86). Those that will segregate tall and dwarf are *SSDdgg* from $C \times A$ and $A \times C$ (cultures 30 75, 30 76, 30 77, 30 78), and *ssDdgg* from $D \times B$ and $B \times D$ (cultures 30 79, 30 80, 30 81, 30 82).

Because earlier studies on hybrids involving types A and F had given unexpected ratios of segregation, the seed for these F_2 generations was obtained in two ways: first, from selfed capsules allowing full time for the pollen tubes to grow (*i. e.* until the style fell off), and, second, from selfed capsules from which the style had been cut off close to the ovary 16–18 hours after pollen had been applied to the stigma. Seeds are not set in this material until 16–18 hours after pollination and then only half-sized capsules are developed with correspondingly fewer seeds and these generally with much lower percentages of germination. The latter set of capsules then

TABLE 13
F₃ GENERATIONS FROM THE MONOHYBRIDS INVOLVING THE HOMOTYOUS TYPES A, B, C, D, TABLE 12 STYLE-CUTTING EXPERIMENTS
COMPARED WITH FULL TIME FOR POLLEN TUBE GROWTH

Culture	Parent plant	Time for pollen tube growth	Length of capsules	Seeds	Seedlings	Per cent germination	S	s	Ratio S s	D	d	Ratio D d	Other forms	Died
F ₃ B X A 30.71	S ₁ DDgg 30.31-4	16-18 hrs.	15-16 mm.	222 (4 capsules)	32	14.4	27	2	13.5	29				3
F ₃ B X A 30.72	The same	Full time	28 mm.	418 (1 capsule)	257	61.5	233	16	14.6	249			1 haploid (S) 1 dwarf, failed to flower	6
F ₃ A X B 30.73	S ₁ DDgg 30.35-61	16-18 hrs.	14-16 mm.	240 (4 capsules)	90	37.5	68	20	3.4	88				2
F ₃ A X B 30.74	The same	Full time	27 mm.	461 (1 capsule)	251	54.4	189	61	3.1	250				1
F ₃ C X A 30.75	S ₁ DDgg 30.33-136	16-18 hrs.	13-15 mm.	346 (4 capsules)	161	46.5	158			111	47	2.4	1 haploid (S)	2
F ₃ C X A 30.76	The same	Full time	25 mm.	470 (1 capsule)	340	72.3	330			259	71	3.6		10
F ₃ A X C 30.77	S ₁ DDgg 30.34-18	16-18 hrs.	13-15 mm.	355 (3 capsules)	175	49.3	170			126	44	2.9	1 dwarf, failed to flower	4
F ₃ A X C 30.78	The same	Full time	25 mm.	493 (1 capsule)	368	47.6	362			270	92	2.9		6
F ₃ D X B 30.79	S ₁ DDgg 30.35-96	16-18 hrs.	10-13 mm.	118 (4 capsules)	13	11.0		13		10	3	3.3		
F ₃ D X B 30.80	The same	Full time	28 mm.	530 (2 capsules)	310	58.5		306		253	53	4.8	2 linear-leaved dwarf, failed to flower	2
F ₃ B X D 30.81	S ₁ DDgg 30.36-7	16-18 hrs.	11-17 mm.	210 (4 capsules)	27	12.8		27		19	8	2.4		
F ₃ B X D 30.82	The same	Full time	26 mm.	419 (1 capsule)	172	40.6		171		124	47	2.6	1 dwarf, failed to flower	
F ₃ D X C 30.83	S ₁ ddgg 30.37-15	16-18 hrs.	14-20 mm.	446 (4 capsules)	163	36.5	155	5	31		160		1 dwarf, failed to flower	2
F ₃ D X C 30.84	The same	Full time	25 mm.	419 (1 capsule)	287	68.5	195	87	2.2		282			5
F ₃ C X D 30.85	S ₁ ddgg 30.38-62	16-18 hrs.	13-20 mm.	388 (4 capsules)	149	38.4	145	2	72.5		147			2
F ₃ C X D 30.86	The same	Full time	25 mm.	345 (1 capsule)	278	80.6	242	26	9.3		268			10

constituted experiments to test the possibilities of competitive pollen tube growth (certation) since the ratios of segregation from this seed in comparison with those from seed normally produced might indicate whether or not the rates of pollen tube growth varied with the different genetic types *S* and *s*, *D* and *d*.

Thus in Table 13 the cultures are arranged in pairs (30 71 with 30 72, 30.73 with 30 74, etc.), the culture from seed after full time pollination following that from seed fertilized 16–18 hours after pollination. Comparisons may then be made between percentages of seed germination, the ratio of *S* to *s* in certain cultures and of *D* to *d* in others. It is assumed that these ratios, if not disturbed by special factors, should be close to the monohybrid ratio of segregation $3 : 1$, which is clearly indicated in some of the cultures. The problem was to determine the factors of disturbance and this proved to be no simple matter.

The ratios of the segregation of tall and dwarfs (Table 13, cultures 30 75 to 30.82), considering the size of the cultures, presented no marked variance from the expected ratio of 3 tall to 1 dwarf. In all cases the ratio of dwarf to tall was as high as or somewhat higher following style-cutting experiments than after full pollination, giving no evidence of a pollen tube growth less favorable to the dwarf. Certainly nothing appeared that would suggest a genetic situation other than segregation from a monohybrid. The total of the tall in these cultures was 1172; that of the dwarfs was 365, a ratio of $3.2 : 1$.

The ratios in the segregation of yellow and sulfur show irregularities that are not easily to be explained. The F_2 of $B \times A$ (cultures 30 71, 30.72) gave yellow to sulfur in a ratio close to $14 : 1$, but the reciprocal cross $A \times B$ (cultures 30 73, 30.74) involving the same parent plants presented a ratio very close to the expected $3 : 1$. In neither case was there marked difference between the ratios from the style-cutting experiments and those of full time pollination, and consequently there was no evidence of slower growth of pollen

tubes of either *S* or *s*. Seed germination in $B \times A$ of 61.5 per cent (Culture 30.72) was too close to the 54.4 per cent in $A \times B$ (culture 30.74) to make probably a differential in seed development. There would seem to be left a possibility that embryo sacs of type *B* introduce factors unfavorable to a full expression of *s* by the hybrid in the competition among megaspores or female gametophytes

The F_2 of $D \times C$ in the certation experiments (culture 30.83) gave yellow to sulfur in the ratio of 31 : 1, a marked deficiency of sulfur plants, while the culture from full time pollinations (30.84) gave a ratio of 22 : 1, not far from expectations on a normal segregation. This definitely suggests a slower growth of pollen tubes carrying *s*. The reciprocal $C \times D$ (cultures 30.85, 30.86) again concerned with the same parent plants presented *S* and *s* in the certation experiment in the ratio 72.5 : 1, and after full pollination in the ratio 9.3 : 1, again suggesting that pollen tubes carrying *s* grow more slowly than do those with *S*.

It is clear that there are some important differences among the types *A*, *B*, *C*, *D* with respect to the relation of *S* to *s* at different points in the life history. The segregation from $A \times B$ and $D \times C$ after full time pollination is close to the expected 3 : 1, but in $B \times A$ and $C \times D$ it is strongly to the disadvantage of sulfur. In the cross $B \times A$ competition to the disadvantage of *s* is apparently expressed at megasporogenesis or between female gametophytes or between developing seeds since style cutting did not modify the ratios of segregation. In the crosses $D \times C$ and $C \times D$ there seems to be slower growth of the pollen tubes carrying *s*.

DIHYBRIDS INVOLVING THE HOMOZYGOUS TYPES *A* AND *D*

The first dihybrids from reciprocal crosses between type *A*, *franciscana*, *SSDDgg*, and type *D*, *franciscana sulfurea nana*, *ssddgg*, were grown at the John Innes Horticultural Institution in the summer of 1925 when selfings and crosses were made which gave the F_2 generations, double reciprocals, and back crosses described in Table 14 and discussed in the

next section of this paper I am deeply appreciative of the facilities extended to me during that summer by Professor Bateson

The parent plants were yellow tall (type A) and sulfur dwarf (type D), both types with red buds. The genes for flower color and for height are in different chromosomes and the crosses are therefore dihybrids with respect to these characters. The cross $A \times D$ (culture 25 31) was represented by 239 plants and the reciprocal $D \times A$ (25 32) by 94 plants. The reciprocals were uniform and indistinguishable both showing complete dominance of yellow over sulfur and tall over dwarf. The hybrids, *SsDdgg*, differed from the dominant parent *franciscana*, *SSDDgg*, in showing greater vigor expressed by somewhat larger leaves and flowers, and they stood somewhat taller in their rows side by side with *franciscana*. The yellow color of the flowers was a shade deeper in the hybrids than in the parents perhaps because of thicker petals. Pollen was perfect in the hybrids as in both parents.

SEGREGATION IN THE F_2 GENERATIONS, DOUBLE
RECIPROCALLS, AND BACK CROSSES INVOLVING
THE DIHYBRIDS $A \times D$ AND $D \times A$.

TABLE 14

In this material we are dealing with the dihybrid *SsDdgg* from reciprocal crosses between type A, *franciscana*, *SSDDgg* and type D, *franciscana sulfurea nana*, *ssddgg*. The cultures as given in Table 14 consisted of the two F_2 generations, the two double reciprocals, and the complete set of back crosses to both parents. The back crosses to *franciscana* (cultures 26 57, 26 58, 26 61, 26 62) expressed complete dominance of yellow over sulfur and tall over dwarf as expected from the genetic purity of *franciscana*. Under each ratio as determined is given the ratio expected on a regular segregation (e.g. R 3 : 1).

From the F_2 generations (26 51, 26 52) and from the double reciprocals (26 53, 26.54) perfect segregation as from a dihybrid should have given 9 yellow tall, 3 yellow dwarf,

3 sulfur tall and 1 sulfur dwarf, or the ratios of 3 yellow to 1 sulfur and 3 tall to 1 dwarf. The actual ratios, Table 14, gave proportions of dwarfs much less than expected and showed a very marked deficiency of sulfur. Since all four cultures consistently express these conditions some combined figures are of interest. The 16 sulfur dwarfs (double recessives) appear in the ratio of 1 : 147 in contrast with the dihybrid ratio of 1 : 15. The 66 sulfur tall are in the ratio 1 : 35 and the 299 yellow dwarfs 1 : 6.9 instead of a dihybrid ratio 1 : 43 (3 : 13). Expressed for the segregation of sulfur and dwarf separately the 82 sulfur plants are in the ratio of 1 : 27.9 and the 315 dwarfs 1 : 6.5 when the dihybrid segregation calls for a ratio of 1 : 3. There was a much greater deficiency of sulfur than of dwarf and the combination sulfur dwarf suffered very much more than either sulfur tall or yellow dwarf.

The four back crosses of the double recessive type D, *ssddgg*, to the dihybrids $A \times D$ and $D \times A$, *SsDdgg*, with complete fertility should give in equal numbers yellow tall, yellow dwarf, sulfur tall and sulfur dwarf (Table 14, cultures 26 55, 26 56, 26 59, 26 60). The results showed marked deficiencies of both sulfur and dwarf, with the double recessive, sulfur dwarf, always much less numerous than either yellow dwarf, or sulfur tall. Combined figures from the four cultures give the 154 sulfur dwarfs relative to all others in the ratio of 1 : 12.9, the 295 yellow dwarfs as 1 : 6.3 and the 325 sulfur tall as 1 : 5.6 where normal expectations called for ratios of 1 : 3. The ratio of sulfur to yellow and of dwarf to tall, assuming complete fertility should be as 1 : 1, but combined figures give the proportions of 1 : 3.5 and 1 : 3.8 respectively. Although sulfur and dwarf suffered about equally when totals are compared there is this interesting distinction. Type D pollinated by the hybrid (26 56, 26.60) gave 173 sulfurs to 231 dwarfs while the hybrid pollinated by D (26.55, 26.59) gave 305 sulfurs and 217 dwarfs, a reversal in relative deficiencies. This would indicate that gametophytes or gametes carrying *s* or *d* have a different relative effectiveness whether male or female.

TABLE 14
F₂ GENERATIONS, DOUBLE RECIPROCALLS, AND BACK CROSSES INVOLVING THE DIHYBRIDS A × D AND D × A R, REGULAR SEGREGATION

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	S	s	Ratio S:s	D	d	Ratio D:d	Other forms	Died
F ₂ A × D 26 31	S ₂ D ₄ g 25 31-1	675	643	98.3	495 yellow tall 101 yellow dwarf 76 sulfur tall 5 sulfur dwarf 617	596	21	28.4 R → 3 1	511	106	4.8 R → 3 1	4 triploids (S) 3 rosettes	19
F ₂ D × A 26 32	S ₂ D ₄ g 25 32-1	648	615	94.9	474 yellow tall 80 yellow dwarf 12 sulfur tall 4 sulfur dwarf 570	554	16	34.6 R → 3 1	486	84	5.8 R → 3 1	4 triploids (S) 1 triploid (s) 2 rosettes	38
(A × D) × (D × A) 26 33	S ₂ D ₄ g × S ₂ D ₄ g 25 31-1 × 25 32-1	638	602	94.4	518 yellow tall 48 yellow dwarf 15 sulfur tall 3 sulfur dwarf 584	566	18	31.4 R → 3 1	533	51	10.4 R → 3 1	1 triploid (S) 1 rosette	16
(D × A) × (A × D) 26 34	S ₂ D ₄ g × S ₂ D ₄ g 25 32-1 × 25 31-1	679	633	93.2	506 yellow tall 70 yellow dwarf 23 sulfur tall 4 sulfur dwarf 603	576	27	21.3 R → 3 1	529	74	7.1 R → 3 1	2 triploids (S) 1 narrow-leaved dwarf 2 rosettes	25
(A × D) × D 26 35	S ₂ D ₄ g × s ₂ d ₄ g 25 31-1 × 25 24-1	631	579	91.8	322 yellow tall 62 yellow dwarf 123 sulfur tall 49 sulfur dwarf 556	384	172	2.2 R → 1 1	445	111	4 R → 1 1	1 narrow-leaved dwarf (S) 1 rosette	21
D × (A × D) 26 36	s ₂ d ₄ g × S ₂ D ₄ g 25 24-1 × 25 31-1	679	523	77	334 yellow tall 34 yellow dwarf 56 sulfur tall 39 sulfur dwarf 507	412	95	4.3 R → 1 1	390	117	3.3 R → 1 1	2 linear-leaved rosettes 1 rosette	13
(A × D) × A 26 37	S ₂ D ₄ g × S ₂ D ₄ g 25 31-1 × 25 31-1	299	266	88.9	259 yellow tall	259			259			1 triploid (S)	6
A × (A × D) 26 38	S ₂ D ₄ g × S ₂ D ₄ g 25 31-1 × 25 31-1	284	259	91.2	253 yellow tall	253			253			1 haploid (S)	5

TABLE 14—(Continued)

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	S	s	Ratio S:s	D	d	Ratio D:d	Other forms	Died
(D X A) X D 26.59	SsDdgg X ssddgg 25.32-1 X 25.24-1	620	593	95.6	377 yellow tall 68 yellow dwarf 95 sulfur tall 38 sulfur dwarf 578	445	133	3.3:1 R → 1:1	472	106	4.4:1 R → 1:1	2 rosettes	13
D X (D X A) 26.60	ssddgg X SsDdgg 25.24-1 X 25.32-1	590	519	88	336 yellow tall 87 yellow dwarf 51 sulfur tall 27 sulfur dwarf 501	423	78	5.4:1 R → 1:1	387	114	3.4:1 R → 1:1	3 linear-leaved dwarfs 1 rosette	14
(D X A) X A 26.61	SsDdgg X SSDDgg 25.32-1 X 25.21-1	368	219	81.7	212 yellow tall	212			212			1 haploid (S) 1 triploid (S)	5
A X (D X A) 26.62	SSDDgg X SsDdgg 25.21-1 X 25.32-1	369	334	90.5	310 yellow tall	310			310			2 rosettes	22

TABLE 15
RECIPROCAL CROSSES BETWEEN TYPES A AND F

Culture	Parent plant	Seeds	Seedlings	Per cent germination	Composition of culture	Other forms	Died
F X A 26.29	ssDdgg X SSDDgg 24.23-2 X 24.21-6	291 (1 capsule)	252	86.6	92 yellow tall green, SsDdgg 134 yellow tall red SsDdgg 226	1 narrow-leaved dwarf yellow green 1 thick-leaved dwarf yellow green	24
A X F 26.30	SSDDgg X ssDdgg 24.21-6 X 24.23-2	242 (1 capsule)	114	88.4	109 yellow tall red, SsDdgg		5

It is clear that the deficiencies of sulfur and dwarf when the hybrid was pollinated by the homozygous type D, *ssddgg*, (cultures 26.55, 26 59) must be due wholly to differentials concerned with the female gametes or gametophytes *SD*, *Sd*, *sD*, *sd*, since the male gametophytes are all of one class, *sd*. Conversely the deficiencies of sulfur and dwarf when type D is pollinated by the hybrid (26 56, 26 60) must result from differentials involved with male gametes or gametophytes *SD*, *Sd*, *sD*, *sd*, since the female gametophytes are uniform, *sd*. All types of gametes and gametophytes function but *SD* much more frequently than the others and *sd* least of all. The differential factor cannot be wholly rate of pollen tube growth nor wholly competition among megaspores and embryo sacs. The factor in common may be that of physiological vigor most strongly expressed through the association of the two dominants *S* and *D* in the class yellow tall, less strongly expressed when only one dominant, *S* or *D*, is present, and least of all through the association of *s* and *d* in the double recessive, sulfur dwarf.

It is interesting to find such clear cut segregation in *Oenothera* material, however difficult may be the understanding of unusual ratios. Attention is called to the not uncommon triploids and haploids listed with the certain narrow-leaved dwarfs among the "Other forms." The triploid parent of my tetraploid *franciscana* (Davis 1933) was one of the four triploids in culture 26 51.

RECIPROCAL CROSSES BETWEEN TYPE A, *SSDDgg*, AND TYPE F, *ssDĠgġ*. TABLE 15

We shall now consider crosses between the homozygous type A, *franciscana*, *SSDDgg*, yellow tall red buds, and type F, *ssDĠgġ*, sulfur tall, green buds, but heterozygous for height and bud color. The latter is the type which appeared in 1914 from the F_2 of a cross *biennis* \times *franciscana* and which has been treated in *Oenothera* literature under the misnomer "*franciscana sulfurea*," a name now properly associated with type B of this paper. The pollen of type F

is somewhat less than 50 per cent good and the chromosome configuration is a ring of 12 and one pair.

The results from reciprocal crosses in cultures expressing complete germination are given in Table 15. Since type F develops two kinds of eggs, $s\widehat{DG}$ and $s\widehat{dg}$, the cross $F \times A$ gives two forms, yellow tall green, $Ss\widehat{DG}\widehat{dg}$, and yellow tall red, $SsDdgg$. The reciprocal $A \times F$ in contrast produces only yellow tall red, $SsDdgg$, because the DG group being linked with a pollen lethal is not inherited through the pollen. There is complete dominance of S and D , and of G when present.

**F₂ GENERATIONS, DOUBLE RECIPROCALLS, AND BACK CROSSES
TO TYPE F OF F₁ HYBRIDS BETWEEN TYPE A,
SSDDgg, AND TYPE F, $s\widehat{DG}\widehat{dg}$ SPARSE
POLLINATIONS COMPARED WITH EXCESS
POLLINATIONS. TABLE 16**

Soon after the establishment of type F, $s\widehat{DG}\widehat{dg}$, in line cultures I began to cross the plant with type A, *franciscana*, SSDDgg, to obtain data on the segregation of yellow and sulfur from F₂ generations, from double reciprocals, and from back crosses of the F₁ hybrids to type F. A full set of such crosses was grown by Professor Shull in 1918 from seed supplied by me and this set of cultures was repeated by me in 1919 from the same lot of seed and in 1920 from seed through other parent plants. Since there were no marked differences between the results recorded by Shull and the repetitions of mine the data have been combined in Table 16. At this time the genetical constitution of type F was not fully known and no observations were recorded on segregation for height and bud color.

With respect to the segregation of yellow and sulfur the ratios were surprisingly irregular with sulfur in numbers very far below expectations. These results led me to repeat the set of crosses using far less pollen than would satisfy the number of ovules and consequently obtaining capsules much smaller than the normal. If pollen tubes carrying sulfur

should grow more slowly than those carrying yellow sparse pollinations might give sulfur gametes an opportunity to express themselves after all of the yellow gametes had functioned. This set of cultures from pollen deficiencies was grown in 1924.

Table 16 gives the results from sparse pollinations compared with the excess pollinations of the earlier cultures in which very much more pollen was applied than was necessary to effect normal development of the capsules. The number of capsules used in each of the deficiency cultures is given together with the range of their lengths and the latter may be compared with the lengths of capsules after excess pollination. It will be seen that the capsules from sparse pollinations were frequently 10–15 mm shorter than the normal and their content of seed was correspondingly smaller. The genetic formulae are given for parent plants and will help to an understanding of the segregation but it must be remembered that *DG* is lethal in the pollen. There is given with the ratios actually found the expected ratios following a regular segregation (e.g. $R\ 3 : 1$). Below are comments on the results presented in Table 16 when sparse pollinations are compared with full pollinations.

$F_2\ A \times F$, from $F_1\ SsDdgg$. Regular segregation of $S : s$ and $D : d$ would be as $3 : 1$. Ratio of $S : s$ following pollen deficiency was $56 : 1$ not so large as from full pollination, $11.1 : 1$, favoring an hypothesis of slower growth of pollen tubes carrying s , but the low per cent of germination after excess pollination may indicate competition among developing seeds to the disadvantage of s .

$F_2\ F \times A$, from $F_1\ Ss\overline{DG}\overline{Dg}$ or $SsDdgg$. The plants selected as parents for the F_2 were green budded, $Ss\overline{DG}\overline{Dg}$. Expected segregation of $S : s$ would be as $3 : 1$ and $G : g$ as $1 : 1$. There was an astonishing scarcity of sulfur the results from sparse pollination being less than from the excess, a low seed germination following excess pollination here did not work to the disadvantage of s . Green budded to red in the ratio of $0.2 : 1$ after pollen deficiency shows a surprising scarcity of the dominant.

TABLE 16
F₂ GENERATIONS, DOUBLE RECIPROCALLS, AND BACK CROSSES TO TYPE F OF F₁ HYBRIDS BETWEEN A, SSDDgg, AND F, siddg
SPARSE POLLINATIONS COMPARED WITH EXCESS POLLINATIONS R, REGULAR SEGREGATION

Culture	Parent plant	Pollination	Length of capsules	Seedlings	Per cent germination	S	s	Ratio S:s	D	d	Ratio D:d	G	g	Ratio G:g	Failed to mature or died
F ₁ A X F ₁ Shull, Davis	SSDggg	Excess	33-39 mm.	691	294	42.5	245	22	11:1 R → 3:1						27
F ₁ A X F ₁ 24.59	SSDggg	Sparse	6 24-27 mm.	1037	975	94	805	144	5:6 R → 3:1	57	15:6 R → 3:1	0	949		26
F ₁ F X A Shull, Davis	SSDGGDg	Excess	30-34 mm.	605	231	38.2	156	3	5:2 R → 3:1						72
F ₁ F X A 24.60	SSDGGDg	Sparse	14 16-25 mm.	855	717	83.9	672	1	67:2 R → 3:1	673	0	116	557	0.2:1 R → 1:1	44
(A X F) X (F X A) Shull, Davis	SSDggg X SSDGGDg	Excess	33-39 mm	753	383	50.9	338	1	338:1 R → 3:1						44
(A X F) X (F X A) 24.61	SSDggg X SSDGGDg	Sparse	12 15-26 mm.	858	761	88.7	721	2	360:1 R → 3:1	723	0	0	723		38
(F X A) X (A X F) Shull, Davis	SSDGGDg X SSDggg	Excess	30-35 mm	414	336	81.1	276	14	19:7 R → 3:1						46
(F X A) X (A X F) 24.62	SSDGGDg X SSDggg	Sparse	7 23-27 mm.	886	637	71.9	542	59	9:2 R → 3:1	601	0	122	479	0.25:1 R → 1:1	36

TABLE 16—(Continued)

Culture	Parent plant	Pollination	Length of capsules	Seedslings	Per cent germination	S	s	Ratio S:s	D	d	Ratio D:d	G	g	Ratio G:g	Failed to mature or died
(A × F) × F Shull, Davis	SsDdgg × ssDdgg	Excess	31-34 mm.	801	462	57.7	295	118	2.5 R → 1						49
(A × F) × F 2463	SsDdgg × ssDdgg	Spare	8 18-20 mm.	332	244	73.7	184	47	3.9 R → 1	60	2.6 R → 1	0	231		13
F × (A × F) Shull, Davis	ssDdgg × SsDdgg	Excess	33-40 mm	844	644	76.3	261	265	1 R → 1						118
F × (A × F) 2464	ssDdgg × SsDdgg	Spare	10 24-29 mm.	919	643	69.9	459	177	2.4 R → 1	567	14.5 R → 3	446	160	2.7 R → 1	37
(F × A) × F Shull, Davis	SsDdgg × ssDdgg	Excess	26-31 mm	361	281	77.8	179	80	2.2 R → 1						22
(F × A) × F 2467	SsDdgg × ssDdgg	Spare	9 14-22 mm	406	314	77.3	235	47	5.4 R → 1	302		33	269	0.12 R → 1	12
F × (F × A) Shull, Davis	ssDdgg × SsDdgg	Excess	32-36 mm	797	500	62.7	356	7	70.9 R → 1						137
F × (F × A) 2468	ssDdgg × SsDdgg	Spare	7 20-26 mm.	411	307	74.7	289	4	72.2 R → 1	293		190	103	1.8 R → 1	14

Double reciprocal $(A \times F) \times (F \times A)$, $SsDdgg \times Ss\widehat{DG}\widehat{Dg}$ or $SsDdgg \times SsDdgg$. The cross grown was $SsDdgg \times Ss\widehat{DG}\widehat{Dg}$ and a regular segregation would be S to s as 3 : 1, there should be no dwarfs or green budded plants. Sulfur was scarcely present, the showing following pollen deficiency being no better than after excess

Double reciprocal $(F \times A) \times (A \times F)$, $Ss\widehat{DG}\widehat{Dg} \times SsDdgg$ or $SsDdgg \times SsDdgg$. The cross grown, $Ss\widehat{DG}\widehat{Dg} \times SsDdgg$, through regular segregation should give S to s in the ratio of 3 : 1 and green buds to red as 1 : 1, there should be no dwarfs. Sparse pollination with S to s as 9 : 2 : 1 gave twice as much sulfur as excess pollinations, 19.7 : 1, seed germination being about equally good, and suggested slower growth of s pollen tubes. Dominant green buds, 0.25 : 1, were again below expectations

Back cross $(A \times F) \times F$, $SsDdgg \times ss\widehat{DG}\widehat{dg}$. Normal segregation would call for S to s and D to d both as 1 : 1. The ratios of S to s from excess pollinations, 2.5 : 1, and from pollen deficiencies, 3.9 : 1, are unfavorable to an hypothesis of slower growth of s pollen tubes. There were about 3 times more tall than dwarfs from pollen deficiencies

Back cross $F \times (A \times F)$, $ss\widehat{DG}\widehat{dg} \times SsDdgg$. Regular segregation should give S to s as 1 : 1, D to d as 3 : 1, and G to g as 1 : 1. Ratio of S to s from excess pollination was almost perfect 1 : 1, but from pollen deficiencies, 2.4 : 1, distinctly unfavorable to an hypothesis of slower growth of s pollen tubes. From pollen deficiencies there were about 15 times more tall than dwarfs and 3 times more greens than reds.

Back cross $(F \times A) \times F$, $Ss\widehat{DG}\widehat{Dg} \times ss\widehat{DG}\widehat{dg}$ or $SsDdgg \times ss\widehat{DG}\widehat{dg}$. The cross grown, $Ss\widehat{DG}\widehat{Dg} \times ss\widehat{DG}\widehat{dg}$, with regular segregation would give S to s and G to g both as 1 : 1. Ratio of S to s from pollen deficiencies was 5.4 : 1 in contrast to full pollinations, 2.2 : 1, again unfavorable to the hypothesis of slower growth of s pollen tubes. There were about 8 times more red than green budded plants in cultures from pollen deficiencies.

Back cross $F \times (F \times A)$, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{Dg}$ or $ss\widehat{DG}\widehat{dg} \times SsDdgg$. The cross grown, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{Dg}$, through regular segregation should give S to s and G to g both as 1 : 1. The ratio of S to s was about 70 : 1 for both sparse and excess pollinations. There were nearly twice as many green as red budded plants from pollen deficiencies.

This set of cultures presents far greater irregularities in the segregation of yellows and sulfurs, talls and dwarfs than those previously described. The segregation was perfectly clear but the reasons for the irregularities in some cases with surprisingly low percentages of sulfur are very difficult to determine. Results from the repetition of the crosses under conditions of pollen deficiency were in most cases unfavorable to the hypothesis of slower growth of pollen tubes carrying s and d , yet the data from style cutting experiments to be described in the next section indicated the contrary. It is possible that severe pollen deficiencies leading to the production of small capsules and a small harvest of seed may introduce physiological disturbances affecting competition between megaspores, female gametophytes and developing embryos, making this line of experimentation far from simple as to its results and unsafe as tests for pollen tube competition.

It is interesting to note that wherever the ratio of s to S is amazingly small as in F_2 , $F \times A$, 1 : 52, $(A \times F) \times (F \times A)$, 1 : 338; $F \times (F \times A)$, 1 : 70.9, the plants of $F \times A$ being the green budded type, the male gametes were SDg and sDG making dwarfs impossible. Sulfur plants from the F_2 of $F \times A$ would be either $ss\widehat{DG}\widehat{Dg}$ or $ssDDgg$, from $(A \times F) \times (F \times A)$ $ss\widehat{DG}\widehat{Dg}$ or $ssDdgg$, from $F \times (F \times A)$ $ss\widehat{DG}\widehat{Dg}$ or $ssDdgg$. These are sulfur talls but not type F , $ss\widehat{DG}\widehat{dg}$. Since sulfur talls were found to be far below expectations in the cultures involving the dihybrids $A \times D$ and $D \times A$, Table 14, it seems probable that the above combinations are particularly unfavorable for survival or that the gamete sDg largely fails to function in these crosses.

Thus from this set of cultures as from those out of monohybrids from the combinations of the homozygous types

A, B, C and D, and out of dihybrids of A and D we find nothing conclusive as to the factors which determine the very irregular and unexpected ratios of segregation. Sulfur rarely approached expectations and sometimes was expressed in such grotesque ratios as some hundreds of *S* to one *s*. The ratios of dwarfs to tall were far below expectations. Green buds although dominant over red sometimes segregated much below and sometimes well above expectations

CROSSES INVOLVING TYPE A, *SSDDgg*, AND TYPE F, *ssDgGg*,
TO TEST THE HYPOTHESIS OF A SLOWER GROWTH
OF *s* AND *d* POLLEN TUBES STYLE-CUTTING
EXPERIMENTS COMPARED WITH FULL TIME
FOR POLLEN TUBE GROWTH. TABLE 17

In the preceding section we have seen that experiments in sparse pollination on crosses involving types A and F generally failed to improve the remarkable ratios of segregation between *S* and *s*, with their marked scarcities of *s*, although pollen deficiencies might be expected to give *s* tubes, should they be of slower growth, an opportunity to fertilize ovules not entered by the *S* tubes. There will now be given some data from experiments on cutting the style above the ovary which do definitely favor an hypothesis of slower growth on the part of *s* tubes. The material, segregating fair proportions of sulfur, deals with the F_2 of $A \times F$, the cross $F \times (A \times F)$ and a direct cross in which two lobes of the stigma of F are dusted with the pollen of A and the other two lobes with the pollen of F. In the course of the studies it was found that no pollen tubes reached the ovary earlier than 15 hours after pollination. The results are given in Table 17.

F_2 $A \times F$, from F_1 *SsDdgg*. Regular segregation of both *S* to *s* and *D* to *d* should be 3 : 1. Full time for pollen tube growth gave a ratio of *S* to *s* as 14.4 : 1, not far from the ratio of 111 : 1 presented by the earlier cultures, Table 16. Cutting the style at 16-18 hours after pollination gave a progeny with only 1 sulfur in a culture of 143 plants from 9

TABLE 17

CROSSES INVOLVING TYPES A, $SSDDg$, AND F, $ssDdg$, TO TEST THE HYPOTHESIS OF A SLOWER GROWTH OF s AND d POLLEN TUBES, STYLE-CUTTING EXPERIMENTS COMPARED WITH FULL TIME FOR POLLEN TUBE GROWTH R, REGULAR SEGREGATION

Culture	Parent plant	Time for pollen tube growth	Length of capsules	Seeds	Seedlings	Per cent germination	Composition of culture	S	s	Ratio S:s	D	d	Ratio D:d	Died or failed to mature
F A X F 23 66-68	$SsDdg$	16-18 hrs.	14-19 mm.	175 (9 capsules)	160	91.4	135 yellow tall 7 yellow dwarf 1 sulfur tall 0 sulfur dwarf 143	142	1	142 R→3	136	7	10.4 R→3	17
F A X F 23-75	The same	Full time	33 mm.	465 (1 capsule)	421	90.5	330 yellow tall 30 yellow dwarf 21 sulfur tall 4 sulfur dwarf 364	359	25	14.4 R→3	360	24	15 R→3	37
F X (A X F) 23 61-63	$ssDdg \times SsDdg$	16-18 hrs.	13-20 mm	432 (18 capsules)	366	84.7	260 yellow tall 27 yellow dwarf 23 sulfur tall 3 sulfur dwarf 313	287	26	11 R→1	283	30	9.4 R→3	53
F X (A X F) 23 65	The same	Full time	33 mm	367 (1 capsule)	297	80.9	198 yellow tall 19 yellow dwarf 42 sulfur tall 5 sulfur dwarf 264	217	47	4.6 R→1	240	24	10 R→3	33
F X A and F 23-73-77	$ssDdg \times SSDDH$ and $ssDdg$	16-20 hrs.	14-20 mm.	785 (21 capsules)	635	80.9	485 yellow tall 9 yellow dwarf 25 sulfur tall 51 sulfur dwarf 570	494	76	6.5 R→1	510	60	8.5 R→3	65
F X A and F 23-79	The same	Full time	33 mm.	591 (1 capsule)	245	84.2	124 yellow tall 11 yellow dwarf 35 sulfur tall 30 sulfur dwarf 200	135	65	2 R→1	199	41	3.9 R→3	45

small capsules. The ratio of dwarf to tall which was 1 : 15 with full time pollination decreased to 1 : 19.4 under the experiment. Seed germination in both cultures was equally high, above 90 per cent. The experiment clearly indicated slower growth of both *s* and *d* pollen tubes.

Back cross $F \times (A \times F)$, $ss\widehat{DG}\widehat{d}g \times SsDdgg$. Regular segregation should give *S* to *s* as 1 : 1 and *D* to *d* as 3 : 1. From full time pollination the ratio of *s* to *S* was 1 : 4.6, not so good as the ratio of 1 : 1 in earlier cultures, Table 16. However, the ratio of 1 : 11 after cutting the style from 18 flowers favored the hypothesis of slower growth of *s* pollen tubes. The ratio of *d* to *D* which was 1 : 10 after full time pollination did not change significantly with the cutting of styles.

Type F, $ss\widehat{DG}\widehat{d}g$, pollinated by both types A and F. This cross differs from $F \times (A \times F)$ in that the male gametes come directly from the types A and F rather than as products of meiosis from the $F_1 A \times F$. Male gametes from types A and F are *SDg* and *sdg* respectively since $s\widehat{DG}$ is eliminated by the pollen lethal from type F. Assuming equal speed of pollen tube growth and fertilization the resultant unions with eggs $s\widehat{DG}$ and *sdg* of type F should give *S* to *s* as 1 : 1 and *D* to *d* as 3 : 1. With similar percentages of seed germination the ratios from full pollination of *s* to *S*, 1 : 2, and *d* to *D*, 1 : 3.9, fell to 1 : 6.5 and 1 : 8.5 respectively following the cutting of styles, suggesting a slower growth of *s* and *d* pollen tubes.

These experiments consistently indicate a slower growth of pollen tubes carrying *s* and possibly *d* whatever other factors may be present to confuse the picture. There is general agreement between the data for the $F_1 A \times F$ and for the same cross listed in Table 16, but not so for the cross $F \times (A \times F)$. The entire set of crosses in Table 16 should be repeated contrasting style-cutting experiments with full time pollinations for the results might show that experiments with sparse pollinations are not safe guides in the study of relative rates of pollen tube growth. It is possible that following sparse

pollination the nutritive conditions within the undersized capsules may be unfavorable to the development of classes of zygotes carrying *s* or *d* in competition with those carrying *S* or *D*

RECIPROCAL CROSSES BETWEEN TYPE E, $Ss\widehat{DG}\widehat{dg}$, AND TYPE F, $ss\widehat{DG}\widehat{dg}$. SPARSE POLLINATIONS COMPARED WITH EXCESS POLLINATIONS. TABLE 18

These crosses are peculiar in that both parents are heterozygous for *D* and *G*, carrying the linked \widehat{DG} allelomorph to \widehat{dg} . In both types \widehat{DG} is inherited only through the egg because it is associated with the pollen lethal

$E \times F, Ss\widehat{DG}\widehat{dg} \times ss\widehat{DG}\widehat{dg}$ Regular ratios of segregation *S* to *s*, *D* to *d*, and *G* to *g* all should be as 1 : 1. Segregation fully expressed would be expected to give in equal numbers yellow tall greens, yellow dwarf reds, sulfur tall greens, and sulfur dwarf reds, but as shown in Table 18 and also in Table 9, yellow tall greens and sulfur dwarf reds were few in numbers. The ratios of *d* and *g* to their dominants is above 1 : 1, an unusual situation further increased by pollen deficiency. Therefore sparse pollination greatly increased the class yellow dwarf red which with normal pollination was far above expectations. Since the functional pollen is all of one class differentials of segregation must be sought on the female side. It will be noted that as the result of crossovers between \widehat{DG} and \widehat{dg} during sporogenesis two plants of yellow tall red appeared in culture 31 81-83

$F \times E, ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{dg}$. Regular ratios of segregation of *S* to *s*, *D* to *d*, and *G* to *g* again should be as 1 : 1. Segregation fully expressed would also be expected to give as in the reciprocal $E \times F$ in equal numbers yellow tall greens, yellow dwarf reds, sulfur tall greens, and sulfur dwarf reds, but the class sulfur tall green (large in the cross $E \times F$) failed to appear and the sulfur dwarf reds were in smaller numbers (Tables 18 and 9). As a result the ratio of *s* to *S* was very small nor was it increased by sparse pollinations. The ratios of *d* to *D* and *g* to *G* were, of course, also modified by the

TABLE 18
 RECIPROCAL CROSSES BETWEEN TYPE E, $S_1D_1G_1d_1$, AND TYPE F, $s_1\bar{D}_1\bar{G}_1\bar{d}_1$ SPARSE POLLINATIONS COMPARED WITH EXCESS POLLINATIONS
 R_1 REGULAR SEGREGATION

Culture	Parent plant	Pollination	Length of capsules	Seeds	Seedlings	Per cent germination	Composition of culture	S	Ratio $\frac{S}{s}$	D	Ratio $\frac{D}{d}$	G	Ratio $\frac{G}{g}$	Ratio or failed to mature
E \times F 31.06	$S_1D_1G_1d_1$ $\times s_1\bar{D}_1\bar{G}_1\bar{d}_1$ 30.05-30 \times 30.06-13	Excess	1 21 mm.	156	166	89.2	1 yellow tall green 55 yellow dwarf red 57 taller tall green 4 taller dwarf red <u>147</u>	61	1.4 E-1 1	58	0.85 E-1 1	56	0.86 E-1 1	19
E \times F 31.01-03	The same	Sparse	14 11-16 mm.	866	475	54.6	4 yellow tall green 301 yellow dwarf red 56 taller tall green 13 taller dwarf red 2 yellow tall red (crossover, pollen 50 per cent bad) <u>417</u>	327	4.3 E-1 1	74	0.515 E-1 1	73	0.51 E-1 1	58
F \times E 31.75-76	$s_1\bar{D}_1\bar{G}_1\bar{d}_1$ $\times S_1D_1G_1d_1$ 30.05-13 \times 30.06-09	Excess	2 22-24 mm.	296	98	23.1	14 yellow tall green 69 yellow dwarf red 1 taller dwarf red 1 yellow tall red (crossover pollen 50 per cent bad) <u>75</u>	74	1 E-1 1	15	0.35 E-1 1	14	0.33 E-1 1	23
F \times E 31.72-73	The same	Sparse	14 14-15 mm.	656	162	24.6	7 yellow tall green 156 yellow dwarf red 2 taller dwarf red 1 yellow tall red (crossover pollen 50 per cent bad) <u>146</u>	144	2 E-1 1	8	0.066 E-1 1	7	0.06 E-1 1	16

absence of sulfur tall greens to the advantage of *d* and *g*, and pollen deficiencies materially increased the very large proportions of these recessives. Two classes of sperms, *Sdg* and *sdg*, would be expected in this cross and a suppression of the *sdg* class would cut out the sulfur tall greens and sulfur dwarf reds, but since the latter occasionally appear there cannot be complete suppression. The results also might come about through failure of seed development on the part of *ssDGdg* suggested by the low percentage of seed development. Crossovers involving *DG* and *dg* again appeared.

It is clear from the peculiarities of these crosses that many of the differential factors affecting segregation must be associated with megasporogenesis, the female gametophyte, or with the development of the seeds. In the cross $E \times F$, with only one class of functional pollen grains, the disturbances must be entirely by way of the female. In the cross $F \times E$ the irregularities might be by way of either male or female or through both. The low percentages of seed germination following $F \times E$ suggest in this cross the possibility of a differential selection through competition among the developing seeds.

CROSSTOVERS

Crossovers affecting the position of *G* in its linked relation to *D* have appeared in this material from the following sources

1. From type E, *SsDGdg*, yellow tall green. There have been recorded 8 yellow tall reds and 11 yellow dwarf greens among 842 plants in cultures from the line of type E (Table 7, cultures 26.75, 27.64, 28.65). The crossovers sulfur tall red and sulfur dwarf green did not appear. Yellow tall reds might arise as the result of crossovers at either mega or microsporogenesis. Yellow dwarf greens could only appear through crossovers at megasporogenesis because of the elimination of *G* in the pollen through its linked lethal. Since the two crossovers have been found together it is probable that both took place during megasporogenesis. The yellow dwarf greens, type G, as would be expected had pollen less

than 50 per cent good. The yellow tall reds showed somewhat less red in their bud cones than *franciscana* and their pollen was only 50 per cent perfect. This type of plant will be considered further.

2 From type F, $ss\widehat{DG}\widehat{dg}$, sulfur tall green. Although crossovers have not appeared in the inbred line of type F, Table 8, a plant of this constitution from the cross $F \times (A \times F)$ gave the remarkably large number of crossovers—9 sulfur dwarf greens and 30 sulfur tall reds in a culture of 189 plants (Table 11, culture 2676). The sulfur dwarf greens had pollen less than 50 per cent good and were type H; they could only have arisen through crossovers at megasporogenesis. All of the 30 sulfur tall reds had perfect pollen and from one of them a culture was grown of 393 plants breeding true, thus indicating that the parent plant had the constitution $ssDDgg$ and was type B. This plant, homozygous for D , could only have arisen through crossovers during mega and microsporogenesis at times such that the gametes sDg might meet.

3 From the cross $E \times F$, $Ss\widehat{DG}\widehat{dg} \times ss\widehat{DG}\widehat{dg}$. This cross has given 7 yellow tall reds, 4 yellow dwarf greens, and 2 sulfur dwarf greens from cultures that totaled 873 plants (Table 9, cultures 2939, 3044, Table 18, cultures 3181–83); sulfur tall reds did not appear. All of these plants had pollen only 50 per cent perfect or less. Yellow tall reds and sulfur tall reds might be expected through crossovers concerned with either parent. Crossovers to give yellow dwarf greens and sulfur dwarf greens could only take place through the female.

4. From the cross $F \times E$, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{dg}$. Out of this cross have come 2 yellow tall reds and 1 yellow dwarf green in cultures of 594 plants (Table 9, culture 2940, Table 18, cultures 3175–76, 3172–73); all plants with pollen only 50 per cent perfect or less. Sulfur tall reds and sulfur dwarf greens did not appear. Yellow tall reds might arise through crossovers concerned with either parent but the yellow dwarf greens would be restricted to crossovers through the female.

Green budded plants from all sources have always presented the 50 per cent or more of bad pollen associated with the presence of *G*, and the studies on pollen germination reported under type E and type F suggest that the pollen lethal is expressed through the bad pollen. The yellow tall red crossovers from type E, from $E \times F$ and from $F \times E$, showing somewhat less red in their bud cones, have pollen only 50 per cent perfect. Assuming that the pollen lethal is responsible for this pollen sterility one would like to conclude that during the crossovers the pollen lethal becomes separated from *G* and follows *D*. Against this hypothesis is the fact that no green budded crossovers have appeared with perfect pollen. Since we know of no form in this material carrying *G* that is free from the pollen lethal it may be possible that the substance of the lethal is so extended in the \widehat{DG} chromosome that a portion follows *D* leaving a remainder with *G* and thus giving pollen lethals to both crossovers.

The frequency of the crossovers affecting \widehat{DG} indicate that \widehat{DG} and \widehat{dg} are in the pair of chromosomes free from the circle of 12 chromosomes in types E and F, and probably in G and H. In these types *S* and *s*, segregating independently of *D* and *d*, must lie in the circle.

SUMMARY

This has been a study of segregation for the most part involving two characters (1) flower color, whether yellow *S* or sulfur *s*, and stature, whether tall *D* or dwarf *d*. The simpler parent types were homozygous with respect to these characters expressed as *SSDD* type A, yellow tall, *ssDD* type B, sulfur tall; *SSdd* type C, yellow dwarf; and *ssdd* type D, sulfur dwarf. These types, having all pairing chromosomes, suggest no cytological peculiarities that might possibly modify an orderly segregation from monohybrids or dihybrids. The expected classes of segregates have been found without exception and some of the ratios have strongly supported the genetical formulae given above. Thus from the monohybrids, as set down in Table 13, *SsDD* from the cross $A \times B$

segregated *S* and *s* in ratios close to 3 : 1, and *Ssdd* from the cross *D* × *C* after full time for pollen tube growth segregated *S* to *s* in the ratio of 2.2 : 1. All segregations from the monohybrids *SSDd* and *ssDd*, Table 13, have presented *D* and *d* in ratios close to the expected 3 : 1. In contrast to this relatively smooth segregation are the deficiencies of *s* in the segregation from *SsDD* out of the reciprocal cross *B* × *A* and from *Ssdd* out of the reciprocal cross *C* × *D*. Style cutting experiments clearly indicated slower growth of *s* tubes in the crosses *D* × *C* and *C* × *D* but not in the crosses *B* × *A* and *A* × *B*. There was no evidence from the experiments that *d* pollen tubes grew more slowly than those carrying *D*. A slower growth of *s* tubes will not account for the deficiencies of *s* in the segregation from *SsDD* out of *B* × *A* and one must consider the possibilities of competition among megaspores, female gametes or developing seeds, factors always to be borne in mind on which it is difficult to get evidence.

The crosses involving *A* and *D*, *SSDD* and *ssdd*, give a dihybrid since *S* and *s* segregate independently of *D* and *d*. There is presented in Table 14 a complete set of segregates from the two *F*₂ generations, the two double reciprocals, and all possible back crosses to both parents. The expected segregates yellow tall, yellow dwarf, sulfur tall and sulfur dwarf have always been present but sulfur plants and dwarfs were far below expectations and the combination sulfur dwarf suffered much more than either sulfur tall or yellow dwarf. The deficiencies of sulfur and dwarf when pollen comes from the recessive, *ssdd*, must be wholly due to differentials concerned with the female gametophytes *SD*, *Sd*, *sD* and *sd* since the male gametophytes are all *sd*. There must also be differentials concerned with a corresponding set of male gametophytes when the hybrid supplies the pollen to the recessive. Experiments on competitive pollen tube growth have not been made with crosses of this latter type.^a The general conclusion can be drawn that *SD* gametes and gametophytes function much more frequently than the others

and *sd* gametes least frequently of all. The results may involve degrees of physiological vigor most strongly expressed when the two dominants *S* and *D* are together in the class yellow tall, less strongly when only one dominant, *S* or *D*, is present, and least of all in the associations of *s* and *d* in the double recessive, sulfur dwarf.

The next set of crosses involved the homozygous type A, *SSDDgg*, yellow tall red buds and type F, *ssDĠgġ*, sulfur tall green buds, heterozygous for height and bud color. Type F has the chromosome configuration of a circle of 12 and one pair. The *DĠ* group is linked with a lethal that prevents its inheritance through the pollen. Therefore, type F although with two kinds of eggs, *sDĠ* and *sdg*, produces only one class of sperms, *sdg*, and the cross $F \times A$ gives two F_1 types yellow tall greens, *SsDĠDġg*, and yellow tall reds, *SsDdgġ*, with the yellow tall reds in greater numbers, Table 15. There is given in Table 16 two sets of F_2 generations, double reciprocals, and back crosses of F_1 hybrids to type F, sparse pollinations compared with excess pollinations. Except for the cross $F \times (A \times F)$, *ssDĠgġ* \times *SsDdgġ*, there were always marked deficiencies of sulfur which was in some cases expressed but rarely. There were also always deficiencies of dwarfs and of the dominant green buds. Sparse pollinations improved the proportions of *s* in only two crosses, the F_2 of $A \times F$ and the double reciprocal $(F \times A) \times (A \times F)$, in the other crosses it worked to the marked disadvantage of *s*. Doubts arise as to the value of experiments on sparse pollinations in relation to the problem of slower pollen tube growth. Sparse pollinations give small capsules and frequently higher proportions of sterile seeds suggesting irregularities of normal physiology that might modify the competition that must be present between megaspores, female gametophytes and embryos.

There must be some extraordinary departure from normal physiological relations within the pistil almost to eliminate the appearance of sulfur plants, Table 16, from the F_2 of $F \times A$, from the double reciprocal $(A \times F) \times (F \times A)$, and from

$F \times (F \times A)$, the plant of $F \times A$ being the green budded type, $Ss\widehat{DG}\widehat{Dg}$. In these crosses the male gametes could be only SDg and sDg making dwarfs impossible. The sulfur plants would all be tall but none of them type F , $ss\widehat{DG}\widehat{dg}$. Such sulfur tallers were found to be far below expectations in cultures involving the dihybrids $A \times D$ and $D \times A$, Table 14, in which type F also was not present. In the above crosses it seems probable that either the gamete sDg largely fails to function or that the sulfur tallers are unable to survive.

From the F_2 of $A \times F$ and the back cross $F \times (A \times F)$ which yield fair proportions of sulfur, Table 16, style cutting experiments presented clear evidence of a slower growth on the part of s and possibly d pollen tubes, Table 17. Full time pollination of the F_1 $SsDdgg$ gave an F_2 with s to S as 1 : 14.4 and d to D as 1 : 15 where expectations called for a 1 : 3 ratio, but cutting the style of nine flowers resulted in only one sulfur to 142 yellows and one dwarf to 19.4 tallers. In the back cross $F \times (A \times F)$, $ss\widehat{DG}\widehat{dg} \times SsDdgg$ full time pollinations gave s to S as 1 : 4.6 (expectations 1 : 1), but style cutting reduced this ratio to 1 : 11. These style-cutting experiments support those on the crosses $D \times C$ and $C \times D$, Table 13, which indicate slower growth of s pollen tubes whatever other factors may be present to confuse the picture.

A final set of reciprocal crosses between types E and F offered the peculiarity that both carried the linked \widehat{DG} associated with the pollen lethal. In the cross $E \times F$, $Ss\widehat{DG}\widehat{dg} \times ss\widehat{DG}\widehat{dg}$, with only one type of pollen, $s\widehat{dg}$, all irregularities of segregation must be concerned with competition at megasporogenesis or among the female gametophytes and developing seeds. The irregularities were great as shown in Table 18. Segregation fully expressed should have given four classes in equal numbers but the dominant yellow tall greens and recessive sulfur dwarf red were scarcely present. Yellow dwarf reds were most numerous and their proportion was markedly increased by sparse pollination with attendant lower seed germination. In the cross $F \times E$, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{dg}$, with two types of pollen, $S\widehat{dg}$ and $s\widehat{dg}$, the expected

segregation fully expressed should have given the same classes as in $E \times F$ and in equal numbers but the class sulfur tall green, large in $E \times F$, failed to appear. This resulted in even higher proportions of yellow dwarf reds further increased by sparse pollinations. A suppression of the sperms sdg would cut out the sulfur tall greens and sulfur dwarf reds, but, since the latter occasionally appear, there cannot be complete suppression. It seems more likely that other factors are concerned, possibly failure of seed development on the part of $ss\widehat{DG}\widehat{dg}$. The low seed germination in $F \times E$ suggests that the disturbances may be largely through competition among developing seeds.

Crossovers affecting G in its linked relations to D have appeared, as described in detail, from type E , $Ss\widehat{DG}\widehat{dg}$, yellow tall green, from a particular plant of type F , $ss\widehat{DG}\widehat{dg}$, sulfur tall green, from the cross $E \times F$, $Ss\widehat{DG}\widehat{dg} \times ss\widehat{DG}\widehat{dg}$, from the cross $F \times E$, $ss\widehat{DG}\widehat{dg} \times Ss\widehat{DG}\widehat{dg}$. Tall reds were common and might arise through crossovers at either mega- or microsporogenesis. They were generally only 50 per cent pollen-perfect, suggesting that the substance of the pollen lethal associated with G is so extended that part of it can follow D and still leave a remainder with G since we know of no plants carrying G that are free from the lethal. A special type of tall red, $ssDDgg$, out of a plant of type F , $ss\widehat{DG}\widehat{dg}$, had perfect pollen and could only have arisen through crossovers during mega- and microsporogenesis at times when the gametes sDg might meet. Dwarf greens can only arise through crossovers during megasporogenesis because of the elimination of G in the pollen through its linked lethal.

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AN INDEX-METHOD FOR COMPARING MOLLUSCAN FAUNULES¹

HUBERT G. SCHENCK AND A. MYRA KEEN

ABSTRACT

The linear coast-line of western North America permits the statement of geographic ranges of Recent molluscan species in terms of latitude. A method of computing index-latitudes for sample collections of mollusks is here devised. By this method, late Pliocene and Pleistocene faunules are correlated directly with Recent assemblages. Fossil faunule "x," with an index-latitude of "n" degrees, can thus be inferred to have lived in an environment much like that of the Recent assemblage at latitude "n." Further interpretation of fossil assemblages depends upon the collection of data for the solution of such problems as stratigraphic zoning, the rate of evolution, and the use of genera as indicators of depth and temperature.

INTRODUCTION

THIS PAPER is a sequel to our previous note² wherein the West Coast of North America was divided, by biometrical analysis, into the following marine molluscan provinces: the Panamic, which has its northern limit at about latitude 23°, the Californian at 48°, the Aleutian at 62°; and the Arctic at about 80°. Between each two provinces is an overlap area of varying width. These provinces are based upon an analysis of the total molluscan fauna (some 2,000 species), so that the conclusions are of little aid in the study of sample littoral faunules, either fossil or Recent. A different biometrical technique must be devised for making comparisons between partial faunas. For this purpose we have found the median of midpoints-of-range to be a servicable index—"index" being used in the statistical sense of "characteristic value."

A midpoint-of-range is the latitude exactly half-way between the two extremes of range of any given species. For a

¹ An abstract of a part of this paper has been published: H. G. Schenck and A. M. Keen, Bathymetric Distribution of Marine Pelecypoda, *Proc. Geol. Soc. Am.* for 1935 (1936), pp. 367-368.

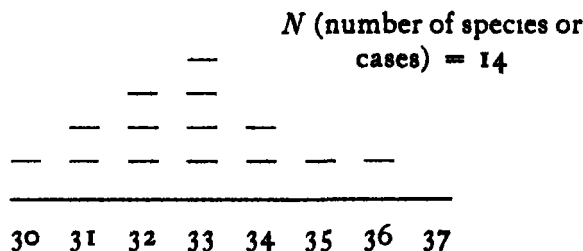
² Hubert G. Schenck and A. Myra Keen, Marine Molluscan Provinces of Western North America, *Proc. Amer. Phil. Soc.*, LXXVI, No. 6.

sample collection of mollusks from any given locality, the *median* of midpoints is the latitude at which, theoretically, the total northward range of species would exactly balance the total southward range. The median is a quantitative statement of trend, for if the majority of species in an assemblage is northward-ranging, the median of that assemblage is necessarily northward-pointing (that is, it falls at a latitude north of the locality of the collection) and *vice versa*.

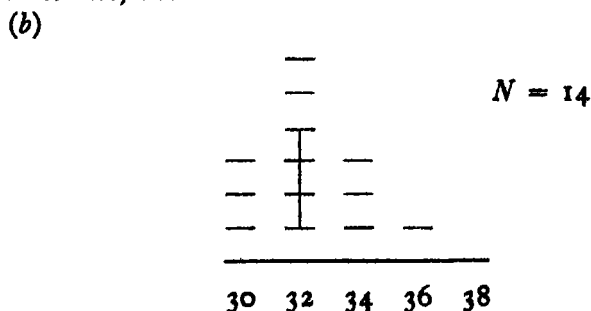
STEPS IN CALCULATION OF THE MEDIAN

The steps in the calculation of these medians are shown graphically in figure 1, and are as follows

- (1) Calculate the midpoint-of-range for each species in the faunal list
- (2) Distribute the midpoints along a horizontal scale, tallying each over its latitude, thus:
 - (a)



If more than 15 to 20 latitudes are represented, it is often convenient to group midpoints by alternate latitudes, thus:



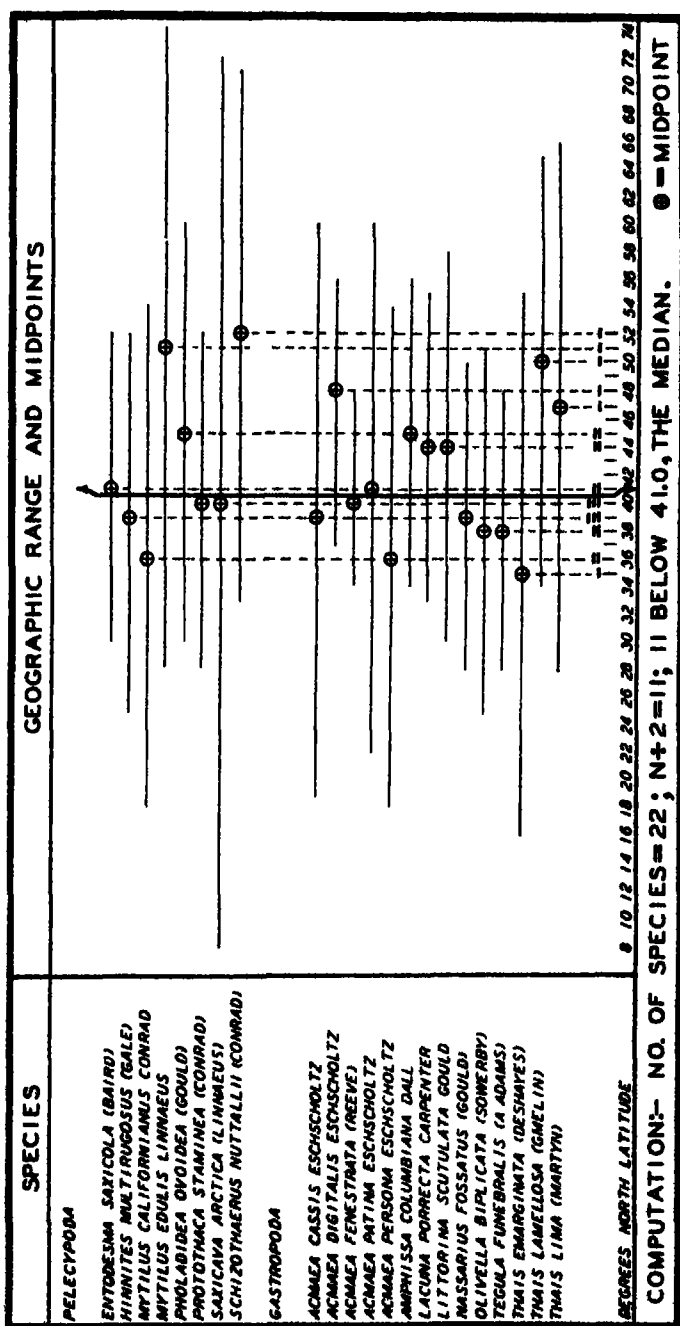


FIG. 1. Graphical illustration of the method of computation of the median of midpoints for a sample Recent collection from near the mouth of Nehalem River, Oregon, latitude 45° 40' N. The total range of each species is shown by the full horizontal line, the circle on each line showing the midpoint. The vertical, broken construction lines show the method of tallying along the latitude scale. Tallying alone is necessary in actual computation. Ranges here and elsewhere in this paper are, in the main, from Dall (1921).

- (3) Since the median is the latitude at which the middle case (species) falls, divide the number of cases (species in the list) by 2.

$$\frac{N}{2} = 7.$$

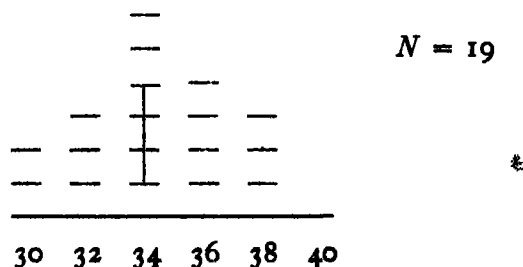
- (4) Determine by inspection, that is, by counting up from the lower or left end of the distribution, the interval containing the middle case—in (a) above, 33, in (b), 32–33. Interpolate in this interval as follows.
- (5) Count the number of tallies below (to the left of) this interval. In (a), 6 occur below 33, in (b), 3 occur below 32.

- (6) Subtract this last result from $\frac{N}{2}$. In (a), $7 - 6 = 1$, in (b), $7 - 3 = 4$.

- (7) Multiply the result of step 6 by the width of the interval (in degrees of latitude), and divide by the number of tallies in the median interval. In (a) $\frac{1 \times 1^\circ}{4} = 0.25^\circ$; in (b) $\frac{4 \times 2^\circ}{7} = 1.1^\circ$.

- (8) Add this quantity to the lower limit of the median interval, thus obtaining the required median, in (a), $33.0 + 0.25 = 33.2^\circ$, in (b), $32.0 + 1.1 = 33.1^\circ$. (The slight discrepancy between these two results, computed from identical data, is due to the small number of cases.)

The following illustrates the procedure in a more complicated distribution, where there is an odd number of cases. (We assume that step (1) has been taken.)



$$(\text{Step } 3) \frac{N}{2} = 9.5$$

(Step 4-5) There are 5 cases below 34.0

$$(\text{Step } 6) 9.5 - 5 = 4.5$$

$$(\text{Step } 7) \frac{4.5 \times 2^\circ}{7} = 1.3^\circ$$

(Step 8) $34.0^\circ + 1.3^\circ = 35.3^\circ$, the median of midpoints

Figure 2 gives the results of the analysis of thirty-three

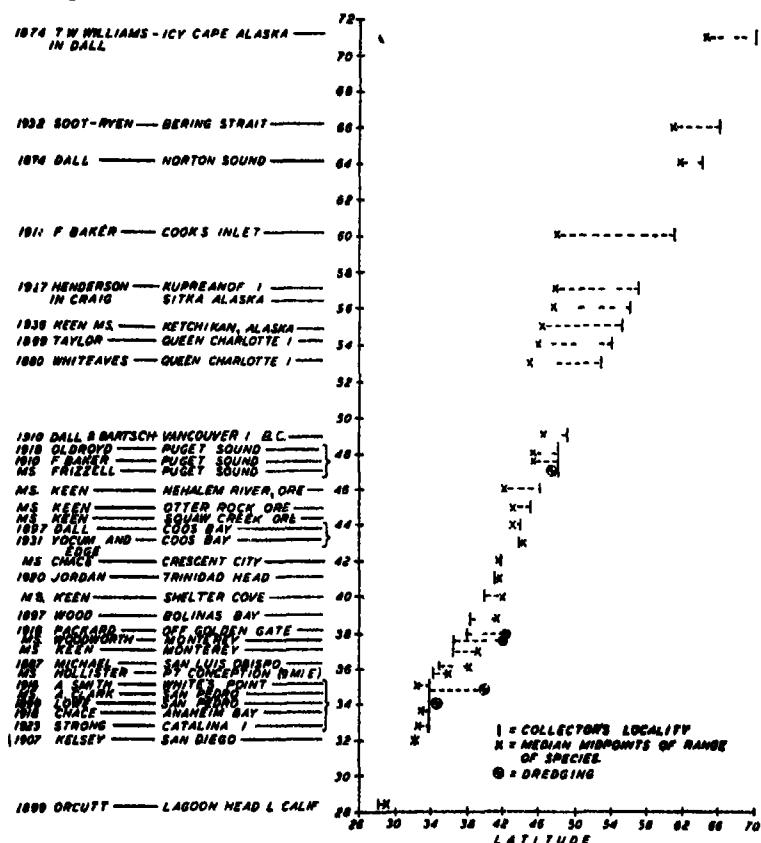


FIG. 2 Relation between median midpoints-of-range of 33 collections of Recent mollusks and the latitude at which the collections were made

lists of collections of Recent mollusks from various points on the West Coast of North America. The lists are spaced

along the vertical axis according to locality, a short bar indicates their placements with respect to the horizontal axis. The disparity between median and collecting locality is shown by a dashed line

Most of these lists represent shore collecting only. Five were from dredgings (maximum depth about 300 fathoms), indicated in the figure by a special symbol. Except for the dredged collections, one notes almost perfect consistency among the lists of figure 2 in the direction which the medians point and in the degree of disparity. San Diego appears to be a center of a littoral district of some kind, the median of the collection there exactly coinciding with the latitude; southward, the single list obtained points northward, and northward the group of Los Angeles (San Pedro) area lists uniformly points southward. Point Conception appears to be the northern boundary of this littoral district, because only a few miles north of there the medians begin again to point northward and so continue up to Trinidad Head, California. The boundary near the California-Oregon line, in contrast to that at Point Conception, seems to be areal, since there are discrepancies among the lists at Trinidad Head and Crescent City, California, and Sisters Rocks and Coos Bay, Oregon, but not in lists to the north or south. Beyond the Alaskan Peninsula in the Aleutian and Arctic provinces, the data though scanty seem to indicate, by the decreasing disparity between median and collector's locality, that the Aleutian Islands constitute another district boundary line.

These littoral districts conform only in a general way to the faunal provinces outlined on page 161, the critical latitudes for the districts being one to several degrees farther south than for the corresponding faunal provinces

FOSSIL FAUNULES

This index-method of analysis of Recent collections yields such uniform results that it can be used safely for the comparison of late Tertiary and Quaternary faunules from the same general area. Figure 3, page 167, lists such an applica-

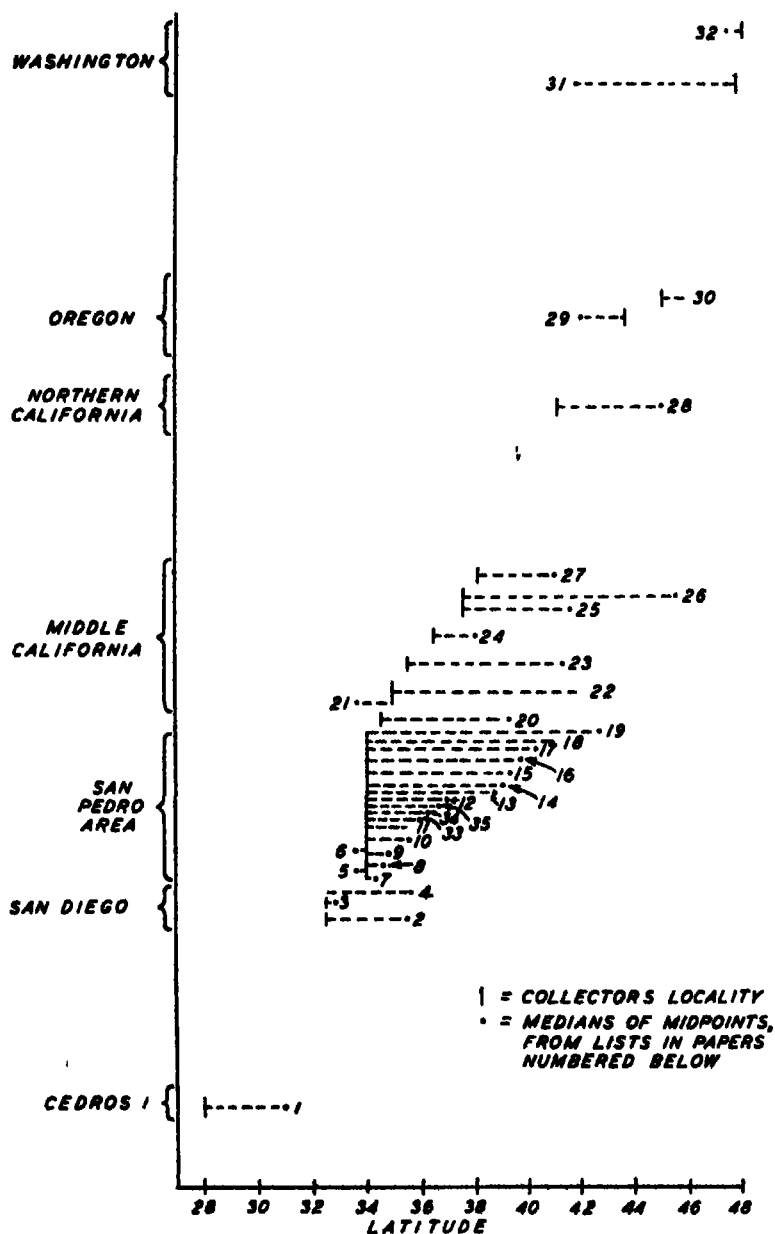


FIG 3 Relation between median midpoints-of-range of 35 fossil collections and the latitudes at which the collections were made

Collection No	Author	Date	Locality	Age
1	Hertlein, L G	1934	Cedros Island	Pleistocene
2	Hertlein, L G	1949	San Diego	Pliocene
3	Hertlein, L G	1949	North Island San Diego	Pleistocene
4	Arnold, R	1963	San Diego	Pliocene
5	Soper, E K and Grant, U S	1932	5th and Hope Los Angeles	Late Pliocene
6	Soper, E K and Grant, U S	1932	6th and Flower Los Angeles	Late Pliocene
7	Pressler, E D	1929	Long Canyon	Pliocene
8	Arnold, R	1903	San Pedro (Upper San Pedro)	Pleistocene
9	English, W A	1914	Elsmere Canyon (Fernando)	Pliocene
10	Arnold, R	1903	San Pedro (Lower San Pedro)	Pleistocene
11	Waterfall, L N	1929	Ventura ("Saugus")	Pleistocene
12	Oldroyd, T S	1984	Nob Hill (Lower San Pedro)	Pleistocene
13	Soper, E K and Grant, U S	1932	4th and Broadway, Los Angeles	Late Pliocene
14	Pressler, E D	1929	Ventura ("Kalamita")	Pleistocene
15	Crickmay, C H	1929	Deadman's Island	Pleistocene
16	Waterfall, L N	1929	Ventura ("Pico")	Upper Pliocene
17	Clark, A	1937	Timm's Point (Bed I)	Pleistocene
18	Arnold, R	1903	Deadman's Island ("Pliocene")	Pleistocene
19	Clark, A	1937	Timm's Point (Bed II)	Pleistocene
20	Grant, U S and Strong, A M	1934	Santa Barbara	Late Pliocene (?)
21	Arnold, R. and Anderson, R.	1907	Fugler Point	Pliocene
22	Arnold, R. and Anderson, R.	1907	One mile north of Schumann	Pliocene
23	Arnold, R. and Anderson, R.	1910	Coalinga (<i>Pecten coalitogensis</i> zone)	Late Pliocene
24	Nomland, J O	1916	Jacalitos	Pliocene
25	Arnold, R.	1906	Santa Cruz (Purisima)	Pliocene
26	Arnold, R.	1908	Santa Cruz	Pleistocene
27	Martin, B	1916	San Francisco (Merced)	Pliocene
28	Martin, B	1916	N California (U Wildcat)	Pliocene (?)
29	Howe, H V	1922	Coos Bay, Oregon (Empire)	Pliocene
30	Arnold, R. and Hannibal, H	1913	Elk River, Oregon	Pleistocene
31	Reagan, A. B	1908	Olympic Peninsula	Pleistocene
32	Arnold, R. and Hannibal, H	1913	Washington ("Saanich")	Pleistocene
33	Cross, R. and Berry, S S	MS	Hilltop Quarry (Lomita)	Pleistocene
34	Arnold, R.	1903	Barlow's Ranch, Ventura	Pleistocene
35	Chace, E P and Chace, E M	1910	Pt Fermin (Upper San Pedro)	Pleistocene

tion comparably with figure 2. For clarity here we have identified authors by number and have placed pertinent data in an accompanying key. Stratigraphic relations have been ignored, the sequence of lists being according to the size of the discrepancy between median and actual latitude. We could not, of course, include faunules older than Pliocene because of the low percentages of living species. The San Pedro-area medians, with only two minor exceptions, are northward pointing, whereas Recent collections in that region are southward pointing. For example, lists 17 and 19, the Timm's Point beds I and II of Alex Clark, have medians of 41.4° and 42.7° respectively. This means that the fossils from these stratigraphic beds correspond to the modern mollusks living in the Cape Mendocino area. Owing to the demonstrated discrepancies between median and collector's locality for Recent collections, we must realize that there is a small

probable error in the implied latitude. So long as we do not attempt a precise statement of water-temperatures, however,⁵ one may neglect this source of error.

Conditions south of San Diego have not changed greatly since the Pleistocene, as far as we can determine from the data available. Certainly no tropical or even subtropical marine fauna is indicated by the single list analyzed from Lagoon Head. Information from northern California to Washington is scanty and somewhat indeterminate; in general, no marked changes are apparent from our data.

The fossil assemblages have average discrepancies between median and actual latitudes about three times as great as those of Recent assemblages. Further research is needed for the interpretation of this fact in terms of past marine temperatures.

CRITICISMS

A pertinent criticism is that of A. M. Strong (verbal communication), who, apparently following Dall (1916), suggests that the chain of islands off California from Santa Barbara to Socorro Island (off Mexico, latitude 19° N.) supports a restricted fauna much more northern in appearance than the mainland fauna of corresponding latitudes. This relationship, should it be verified, would not necessarily invalidate the index-method, but would necessitate certain modifications of the range-data were we to attempt absolute placement of fossil faunules on a Recent latitude-scale. We do not, however, believe that a statement of absolute conditions, such as postulation of water-temperatures for fossil faunules, is at present possible or desirable. The analysis (Fig. 3) is intended only to show that the conditions of deposition for a given fossil faunule approximated the conditions of the present-day coast at the latitude indicated more nearly than did those of the two faunules listed above and below it.

There are, of course, alternatives to the method of analysis proposed here. One such is that used by U. S. Grant, IV,³

⁵ In a paper entitled "Summary of the Marine Pleistocene of California," read before the Cordilleran Section, Geological Society of America, Stanford University meeting, April 13, 1935.

who plots actual present-day ranges of species in fossil lists against a map of the West Coast of North America and deduces probable water-temperatures by inspection of the overlap of ranges. We question the utility of this method because it is open to the criticism of incorrect range-data in twice as great degree as the median-of-midpoint method (the middle of an altered range would suffer only half as much change as an endpoint); and, more important, because in order to use present-day shore water-temperatures as indicators of past conditions, the investigator must prove that every species the range of which includes the overlap area is capable of living in the exact location at which the temperature record was made. The range of a northern species, for example, may indeed overlap the range of a southern species at San Pedro. But the northern species may be found only in very deep, cold water off shore, while the southern species may occur only in favorable near-shore conditions where the temperature is relatively high. Mere overlap of range is meaningless in such a situation

RELIABILITY

At least two objective checks on the reliability of the index-method are possible: (1) repeated sampling from a single locality, the medians of which should be approximately identical; (2) sampling from a single latitude at varying depths (such medians should vary in direct proportion to varying depth) Inspection of figure 2 shows that both conditions are satisfied—that is, (1) medians from identical localities, for example, San Pedro or Puget Sound, are either identical or differ by less than one degree of latitude; (2) the deep-water dredging of Alex Clark in Catalina channel has a much greater disparity between median and actual latitude than the nearby shallow-water dredging of Lowe

Several other advantages of the method may be cited in addition to high reliability. (1) misidentifications do not carry so much weight as they may in qualitative analyses, but affect the median only if they occur in species the midpoints of which are at or near the median of the group, (2) the median

is an index of an assemblage as a whole, and is little affected by adventitiously introduced species—ballast shells, reworked fossils, etc.; (3) it affords a convenient, concise statement of trend uninfluenced by the biased selection which occurs when “characteristic” species of a faunule are named. One may argue, of course, that some species are of much more value than others for the interpretation of faunules—that the presence of a single specimen of *Ostrea* or *Anadara* might be of more value in deductions than would the presence of a hundred less diagnostic forms. This we are entirely willing to grant, but with the important reservation that before such species are allowed to influence or dictate a conclusion, every one of the hundred other species must be *proved* to be non-diagnostic. Otherwise, there is always the possibility that diagnostic species of a diametrically opposite sort are present in the assemblage but have escaped attention. Until, for any faunule, the diagnostic significance of certain species is clearly established, quantitative analysis remains less open to unsuspected error than qualitative

UNSOLVED PROBLEMS

Introduction —It is the purpose of this paper to show that even with incomplete and inaccurate data, a problem such as geographic distribution can be approached objectively and that such an attack may yield reliable and pertinent results. We may infer also that not only geographic distribution but a long list of other problems might be so approached. Thus, both the temperature and the bathymetric range of the genera of the Mollusca might be analyzed statistically with significant results. A statement of these and other unsolved problems which might profitably be subjected to such study is not out of place here.

Temperature Indices.—Temperature has long been used as a criterion for classifying assemblages, as by Arnold (1903), Packard (1917), and many others. The usual procedure is to determine whether each species in a faunal list is predominantly northward or predominantly southward ranging, to

compute the per cent of species in either category, and then to decide on the basis of the percentages the temperature-condition indicated. The defect of this method is that inadequate range-data may lead to serious errors of interpretation, as in the study by Packard (1918 *a*, p. 233), who concluded, "The majority of the entire outside fauna [off Golden Gate] as known from the 'Albatross' collections are predominately southward ranging," and that "the list of prevalent species for the [San Francisco] bay and for the different divisions of the bay does not contain a single predominately southward ranging form . the bay fauna as a whole also has a northern aspect " Retabulation of his data, however, with corrected ranges shows that actually the proportion of northward and southward ranging species in the two faunas is nearly identical, the dominant tendency being rather (though very slightly) in the direction opposite to Packard's conclusions Of the outside fauna, 75 per cent are northward ranging, 22 per cent southward, and 3 per cent restricted to the area, of the inside fauna, 71 per cent are northward ranging, 25 per cent are southward ranging, and 4 per cent are restricted

Further, use of the concept "northern" or "southern" may stimulate the student to search for an explanation where none is needed or to advance an explanatory hypothesis at variance with facts For example, when "northern" forms are found in the same fossil assemblage as "southern" ones, the biostratigrapher invokes some such hypothesis as that exceptionally heavy storm waves have cast up shells from deeper (colder) water and mixed them with the warm-water assemblage Recently in Japan there was an exceptional wave that should have fulfilled the conditions of this hypothesis, but the shells that were thrown up, according to Nomura and Hatai (1935), were all littoral species The discrepancy between supposed cold and warm water genera in the same assemblage is more probably explained by the fact that actual temperature records for living species are altogether too incomplete.

Finally, it is of outstanding importance to the biostratigrapher that he devise some objective means of determining a generic index to water temperature, in order that early Tertiary and perhaps late Mesozoic faunules can be studied and temperature trends can be worked out. One illustration of the vagueness of subjective methods is taken from Clark (1921, p. 611). This statement is fairly typical of the deductions current in paleontological literature.

"The fauna from the Wildcat and Merced of northern and middle California is essentially boreal in character. In southern California the Pliocene is for the most part represented by a fairly warm-temperate fauna. These two faunas, the boreal and the warm-temperate, have very little in common, and consequently it was a long time before their contemporaneity was recognized. The solution of the problem was obtained from the fauna of an intermediate area. The fauna of the type section of the Purisima in the Santa Cruz Mountains of California is in part warm-temperate and in part boreal, and certain species very common in the north, some of which are fairly highly ornamented forms, were found in this section."

What does the term "boreal" mean? If, as it is generally used, it means a cold-water condition approaching that of Arctic regions, then the conclusions reached by Clark are open to question, for analysis of the Wildcat faunule indicates (list 28 in figure 3) that it has a median of 45.0° , which is well within the limits of the California province. The median of the Merced beds is 40.0° , and of the Purisima near Santa Cruz, 41.0° . From the evidence given in the quotation above, we can make no comparison with southern California, for we do not know which beds the author included in his Pliocene.

Bathymetric Indices—Likewise needed are more precise data on the bathymetric distribution of genera before any one genus, no matter how defined, can be utilized as a certain indicator of the depth at which sedimentary rocks were laid down. We present two cases to illustrate the nature of the problem.

Pleurotomaria has been said to prove "deep-sea" conditions, and the Danian beds in Denmark have been interpreted as a deep-water deposit largely because of the abundance of

representatives of this genus. However, a specimen of *Pleurotomaria* (*Entemnotrochus*) *adansoniana* Crosse and Fischer in the British Museum (No G 26243) was taken in 60 fathoms off Barbados. This gastropod, therefore, cannot be said to be a sure index of deep water.

Dickerson (1913, pp 265-267) analyzed certain Eocene fossils from Marysville Buttes, California, and concluded that the strata were laid down in water about 100 fathoms deep. If one takes his data at face value and plots them graphically, one finds that he could have concluded, with equal reason, that the fossiliferous strata were laid down in waters either 80 or 40 fathoms in depth, or even less. As a matter of fact, his bathymetric data were incomplete. Moreover, had he not omitted in his deductions such genera as *Ostrea* and *Solen* (his identifications), he would, perhaps, have favored a depth considerably less, for these genera are generally considered to be "shallow water" bivalves.

The unreliability of genera as at present defined and with our present information is shown in figure 4, a graph that represents a reconnaissance of what a more detailed investigation would show. This preliminary survey is based upon data taken from Cooke (1895), Cotton (1930), Dall (papers cited in bibliography), Dautzenberg (1927), Fischer (1887), Hatai (1936), Hertlein (1935), Johnson (1934), Melvill and Standen (1907), Prashad (1932), Schenck (1934), Smith (1885), Taylor (1899), Thiele and Jaekel (1931), Verrill (1884, 1885), Verrill and Bush (1898), Verco (1907-1908), and Woodring (1926). The number of genera employed and the literature consulted should be a fair sample for statistical treatment.

The heavy vertical lines in figure 4 represent bathymetric ranges of 117 genera and subgenera. Latitude and longitude are disregarded, not only because three-dimensional information is with difficulty arranged on a single plane, but also because a bathymetric classification, to be of utility to the biostratigrapher, must consistently assort genera on the basis of differential depth-range alone. Therefore, all possible known occurrences of a wide sample of genera must be com-

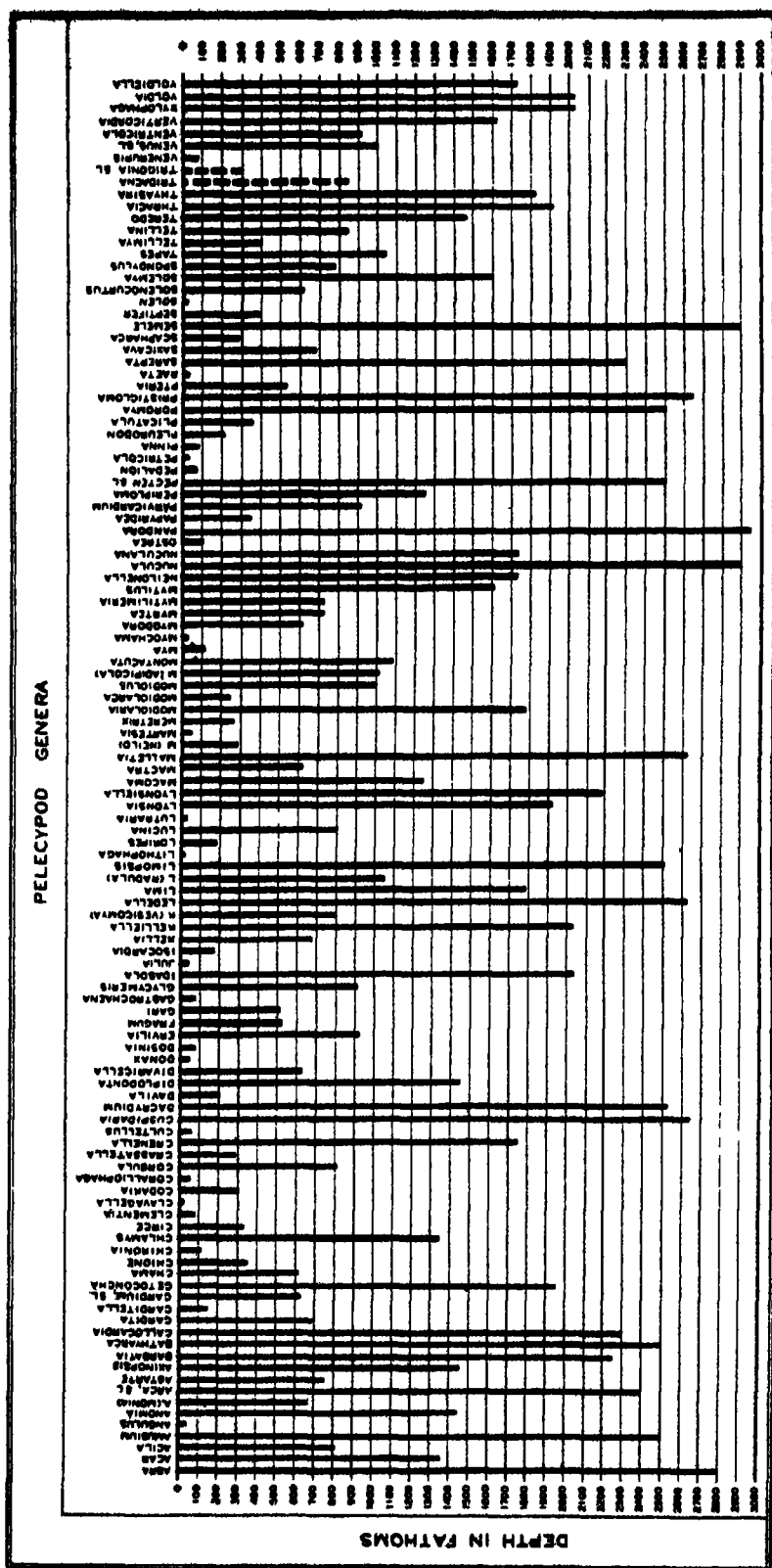


FIG. 4. A preliminary graphical analysis of the bathymetric distribution of certain pelecypod genera

piled before a standard index of the depth-range of any given genus can be established

Reliable conclusions regarding bathymetric distribution *per se* would require data which are reasonably complete and in which the identifications are accurate, depths precisely determined, and the possibility of reworked shells from pre-Recent deposits eliminated. To compile such data for the Pelecypoda alone would be a task beyond the scope of this paper, and to complete the work by obtaining a similar mass of information on Gastropoda would require years of research. Granting, however, the tentative nature of the analysis in figure 4, certain deductions may be justified.

Only a small percentage, about 15 per cent, of genera are restricted to waters less than 100 fathoms deep, many genera taken by geologists to indicate "shallow water" come from depths considerably greater than this. A fairly high percentage, 41 per cent, of the pelecypods are reported to extend to depths below 1,000 fathoms. These "deep-water" bivalves include representatives of many genera and subgenera (some are not named in figure 4), such as the following: *Abra*, *Acar*, *Amussium*, *Anomia*, *Barbatia*, *Bathyarca*, *Callo-cardia*, *Cetoconcha*, *Chlamys*, *Crenella*, *Cuspidaria*, *Dacrydium*, *Diplodonta*, *Hyalopecten*, *Idasola*, *Kelliella*, *Ledella*, *Lima*, *Lima (Radula)*, *Limea*, *Limopsis*, *Lyonsia*, *Lyonsiella*, *Macoma*, *Malletia*, *Modiolaria*, *Myonera*, *Neilonella*, *Nucula*, *Nuculana*, *Pandora*, *Pecchiola*, *Periploma*, *Poromya*, *Pristigloma*, *Pseudamussium*, *Sarepta*, *Scrobicularia*, *Semele*, *Solemya*, *Tapes*, *Tindaria*, *Thracia*, *Thyasira*, "*Venus*," *Verticordia*, *Vesicomya*, *Xylophaga*, *Yoldia*, *Yoldiella*.

When the genera named in figure 4 are grouped in their respective orders using the classification of Pelseneer, it appears that 46 per cent of the Protobranchiata range deeper than 2,000 fathoms, the Filibranchiata are about equally distributed as to range; of the Eulamellibranchiata, 74 per cent

⁴ Some of the names in this list and in figure 4 have been changed by one author or another. Thus, some believe that *Taras* has priority over *Diplodonta*, *Musculus* over *Modiolaria*, *Alويدs* over *Corbula*, etc. "*Solenomya*" is an unjustified emendation of the prior name, *Solemya*. *Pleurodon* S. Wood, 1840, is a primary homonym of *Pleurodon* Harlan, 1831. These nomenclatural matters cannot be taken up here.

are confined to depths of less than 1,000 fathoms; and of the three genera of Septibranchiata, one (33 per cent) extends below 1,000 fathoms and two (67 per cent) below 2,000 fathoms. The same data may be summarized by depths as follows: of the genera limited to depths of less than 1,000 fathoms, the largest proportion (80 per cent) are eulamelli-branches; of those whose ranges end between 1,000 and 2,000 fathoms, eulamelli-branches again predominate (52 per cent), of those genera ranging beyond 2,000 fathoms, the majority (39 per cent) are Filibranchiata.

These data suggest that the Pelecypoda are eurybathyal organisms, not greatly sensitive to changes in vertical distribution, which is in harmony with our previous finding that West American Pelecypoda are eurythermal.⁵ We conclude that by the customary method of approach (the method utilized here), it is at present impossible to devise a generic depth-index for the pelecypods. An alternative method such as that of Woodring (1928, p. 33) might be a better means of attack, though impracticable on a large scale.

Stratigraphic Zoning.—The statistical index-method described in this paper might be applied to a zonal division of the stratigraphic column in an area of uniform lithology. This application of the study was suggested to us by Hollis D. Hedberg. Numerous borings through continuously foraminiferal Upper Tertiary sediments in Venezuela, for instance, show that there is a gradual change in the character of the foraminiferal fauna with depth, so that although the assemblage at 6,000 feet may be entirely different from that at 2,000 feet, there is still no sharp line of division between the two faunas. When zonal divisions are not obvious, a quantitative analysis might be employed to advantage, particularly in correlating isolated outcrop samples with some part of the well-sections.

Rate of Evolution.—No one has collected exact data concerning the rate of evolution of the molluscan species in the eastern North Pacific Ocean. The small percentage of extinct

⁵H. G. Schenck and A. Myra Keen, Marine Molluscan Provinces of Western North America, *Proc. Amer. Phil. Soc.*, LXXVI, No. 6.

species in the early Pleistocene deposits of California suggests that the modern species have endured unchanged for an appreciable length of time—more than 25,000 years, but several factors need to be studied objectively. Little is known, for example, about variations induced by environmental conditions, in spite of many vague and philosophical assertions. We feel that generalization about morphologic changes in the organisms of the past is unjustified before a series of objective control studies of living species is attempted.

CONCLUSIONS

The application of the median-of-midpoints method of biometrical analysis to fossil faunules calls for revised interpretations of certain Pacific Slope Pliocene and Pleistocene assemblages north of Lower California, for none of these is truly tropical or truly boreal when compared with corresponding Recent assemblages. For example, the coldest-water Quaternary faunule in California indicates marine conditions no colder than those of northern Oregon of today. The fact, however, that the fossil faunules differ from the Recent in their somewhat greater discrepancy between median and collector's latitude suggests a shifting of thermal-area boundaries since mid-Tertiary time

Finally, this investigation suggests a method of approach to certain difficult questions. The use of genera as indices of temperature and depth of water is shown to be unwarranted at the present state of our knowledge. The outstanding need is a more painstaking collation of facts than has yet been attempted. Other problems which merit objective treatment are stratigraphic zoning and the rate of evolution of marine mollusks. Each of these problems can be solved satisfactorily by objective methods, and particularly by the use of control studies on living forms.

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STUDIES ON *IODAMŒBA BÜTSCHLI* (PROTOZOA) WITH SPECIAL REFERENCE TO NUCLEAR STRUCTURE

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Abstract

Iodamaba bütschli was found in 153 per cent of 1700 human hosts and in 45.45 per cent of 55 apes and monkeys examined.

Trophozoites ranged in diameter from 4 to 19 microns, and cysts from 7 to 13 microns. There is some evidence for the existence of a small race.

In the relatively large vesicular nucleus of the trophozoite there is normally a large, smoothly rounded, centrally located endosome surrounded by the vesicular space in which the perienosomal granules form a single layer about midway between the endosome and the nuclear membrane. Variations in the endosome consisted of irregularities of size and shape, vesiculation, fragmentation and extrusion of globules into the vesicular space. Variations of the perienosomal granules consisted of differences in size, number and position or even their apparent absence. In the cysts the perienosomal granules normally aggregate into a crescent-shaped group at one side of the endosome. Variations consisted of dispersion of the granules of the crescent to various positions within the nucleus and vesiculation or fragmentation of the endosome.

Chromatoid material, either as diffuse stainable material or in the form of definite bodies, is recognizable in addition to the small rounded "volutin" granules.

Schaudinn's fluid and its more common modifications gave satisfactory fixation for both trophozoites and cysts. Addition of 10 per cent to 20 per cent of glacial acetic acid to Schaudinn's fluid tended to cause the endosome to lose its stainability in the cysts but not in the trophozoites. Bouin's fluid and its modifications gave fairly satisfactory fixation for the trophozoites but not for the cysts. Alcoholic Bouin's caused "buds" to be formed on cysts. Haemalum stained the endosome more lightly than did iron-haematoxylin but stained the perienosomal granules intensely.

The perienosomal granules are thought to constitute the chromosomal chromatin but definite determination of this point must await the working out of nuclear division in detail.

I INTRODUCTION

According to Dobell (1919) the discovery that amœboid protozoa live in the human intestine was made by Lewis as long ago as 1870, yet there are many problems still to be solved in connection with the group of amœboid species now known to live in the digestive tract of man as well as in that of a great many other animals (see Wenrich, 1935). It took more than a quarter of a century to establish the fact that there are two species of larger amœbæ in the human colon and that one is capable of producing disease while the other is

relatively harmless. In the decade between 1910 and 1920 there arose an appreciation of the fact that there are several smaller species that live in the same habitat. Now, six species, at least, are recognized as parasites of man. These are *Endamæba gingivalis*, found in the mouth, and five others, located in the large intestine, namely, *Endamæba histolytica*, *E. coli*, *Endolimax nana*, *Dientamæba fragilis* and *Iodamæba bütschlii*.

For this group of endozoic amœbæ, separation into genera is based primarily upon the structure of the nuclei. Hence, a study of nuclear structure and its variations is important in relation to the making of diagnoses of these amœbæ.

Variation is one of the most common of the characteristics of living things, therefore it is highly important to determine the range of variation for each species and to determine the extent of overlapping in the characters of related species. I have undertaken a study of nuclear structure and nuclear variation in these endozoic amœbæ and the present communication is one of a series that it is hoped to prepare on these subjects.

It should be emphasized that studies of nuclear structure in these animals depend upon the preparation of fixed and stained slides. Consequently, methods of technique play a very important part in the success or failure of such studies. Considerable attention has therefore been given to the matter of technique, especially to the effects of different types of fixing agent.

This study has been aided by grants from the Special Research Fund of the University of Pennsylvania and by a grant from the Penrose Fund of the American Philosophical Society.

II SOURCE OF MATERIALS

This study of *Iodamæba* is based in part upon 26 cases of infection in man that have been found during the course of routine examinations for intestinal protozoa and during the course of various protozoological surveys, the total number of persons examined being 1700. For assistance in procuring

this material I am indebted to a number of people but more especially to Dr John H Arnett. Dr R M Stabler has assisted in the examination of this material The second source of material has been 25 infected anthropoids out of 55 from which specimens have been obtained in recent years, especially at the Zoological Garden of Philadelphia and at the home of Mr. Warren E Buck, importer of wild animals from Africa Apes and monkeys positive for *Iodamæba* were four rhesus monkeys, three Kra monkeys, two green monkeys, two African mangabey monkeys, one Mona monkey, one Japanese macaque, three mandrills, one Anubis baboon, one Gelada baboon, five chimpanzees and one gorilla For kindness and assistance in procuring this material I am indebted to Dr Herbert Ratchliffe, Assistant Pathologist at the Philadelphia Zoo, Mr. Warren E. Buck, Dr Q M Geiman, Dr R M Stabler and Mr Levon Terzian.

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III. OBSERVATIONS

A. General Morphology

I Size — *Iodamæba bütschli* is usually described as being intermediate in size between the larger *Endamæba histolytica* and *E coli*, and the smaller *Endolimax nana* and *Dientamæba fragilis*. The range of size is considerable, however, overlapping the size ranges of both the larger and smaller species, as the measurements given below will show These measurements have been made with an ocular micrometer, the cells being measured consecutively as they came into the microscopic field while the slide was being manipulated with a mechanical stage. The measurements of diameters are given. For the non-spherical cells the average of the length and width is given.

In one human case where there were a small number of trophozoites (Figs 1-3) among a great many cysts (Figs.

5-16), 100 trophozoites averaged 10.2 microns with a range from 6 to 15 microns. Another set of measurements of 50 trophozoites gave an average of 9.9 microns and a range from 8.0 to 12.5 microns. One set of 100 cysts measured from this case gave an average of 10.26 microns with a range from 8.00 to 12.50 microns. Another set of 100 cysts gave an average of 10.2 microns with a range from 8.0 to 13.0 microns.

From another human case, 100 trophozoites from a slide fixed in modified Bouin's fluid (Figs. 37-42, 46, 48) gave an average of 13.51 microns with a range from 9.50 to 19.00 microns. From another slide, fixed in Schaudinn's fluid plus 5 per cent of acetic acid, the average for 100 trophozoites was 11.27 microns with a range from 7.00 to 14.00 microns. From these measurements it would seem that Schaudinn's fluid causes more shrinkage than does the modified Bouin's fluid. Measurement of 100 cysts from a different fecal specimen from the same host gave an average of 10.11 microns with a range from 8.00 to 12.50 microns. In these two cases the cysts are as large as, or only slightly smaller than the trophozoites.

In a third human case 100 trophozoites (Figs. 17-26) averaged 5.58 microns with a range from 4.00 to 10.00 microns. The modal diameter in this series of measurements was 5 microns. From the same slide 100 trophozoites of *Dientamoeba fragilis* averaged 8.85 microns with a range from 5.00 to 12.00 microns. The measurements suggest a small race of *Iodamoeba*. These small trophozoites were found in the sixth stool from this host and there were no cysts present. Neither trophozoites nor cysts were detected in most of the other stools, although there were a few cysts in the third one, from which 25 cysts (Fig. 62) were measured. They gave an average of 7.94 microns and the range was from 7.00 to 10.00 microns. While the evidence for the existence of a small race of *Iodamoeba* is rather striking, one should not be too hasty in drawing such a conclusion. Very small individuals and very small cysts are occasionally met with in other cases where the great majority of individuals are of a typical size. For

example figure 63 illustrates a small trophozoite, 5.7 by 4.3 microns, and figure 64 a small cyst, 7.0 by 6.0 microns from the same case from which all the drawings on plate I were made. Some unusual circumstance might account for an unusual number of small trophozoites and small cysts in the case from which figures 17-26 and 62 were taken. It is interesting that trophozoites usually range to a lower limit of size than do cysts.

Fecal samples from two chimpanzees provided trophozoites but practically no cysts. Both were young animals just brought over from Africa by Mr Warren E. Buck. Measurement of 100 trophozoites (Figs 27-36) from one of these hosts gave an average of 11.7 microns and a range from 7.0 to 18.5 microns. The largest trophozoite seen in this study was from this host and measured 24.0 by 16.0 microns. Measurement of 100 trophozoites from the other chimpanzee gave an average of 11.03 microns with a range from 7.00 to 15.00 microns. These two averages agree closely with the averages of 11.27 and 10.20 microns for two human hosts when the same fixation was used on the slides.

2. *The Trophozoites*—In life the trophozoites are rather sluggish but move about by the extrusion of clear ectoplasmic pseudopodia. The nucleus is not usually visible but a variety of food bodies are commonly present, sometimes in considerable quantity (Figs 38-44). On stained slides the ectoplasmic layer may be clearly differentiated (Figs 40, 42, 43, 46, 48), but more commonly it is not (Plate II). The protoplasm may enclose a considerable number of vacuoles in addition to those containing food (Figs. 30-36, 67, 68).

No clearly recognizable division stages have been seen in this study although figure 67 shows a nucleus with two endosomes suggesting some stage in division.

3. *The Cysts*—The cysts of *Iodamæba* are notably irregular in profile and are thus strikingly different from the more rounded cysts of other endozoic amœbæ. When stained with iodine a majority of the cysts show a sharply demarkated area containing an apparently homogeneous mass

which stains deep brown in color. This is the glycogen body and its prevalence led to the characterization of these cysts as the "iodine cysts". In preparing fixed and stained slides the glycogen is dissolved out leaving a vacuole which, however, often displays a fine network of fibrils through it (Plate IV).

In addition to the glycogen vacuole the stained cyst commonly displays some chromatic material in the cytoplasm which is highly irregular in amount and appearance. Figures 4, 7 and 8 show the tendency for the chromatoidal material to be disposed in strands or layers just outside the glycogen vacuole. Figures 54 and 60 show irregular masses of this material while figures 49 and 58 show it in a sort of network. Figure 51 shows a strand as an irregular spiral and figure 52 shows a pair of long slender bars which curve about the glycogen vacuole. In addition to these more or less irregular masses, or without them, there may also be a larger or smaller number of rounded granules of deeply-staining volutin-like material (Figs. 6-8, 10-12, 14, 16, 52).

B The Nucleus

1. *Size*—The nucleus of *Iodamæba* is relatively large but is subject to rather wide variations in size. In the animals represented by the accompanying illustrations, for example, the diameters range from 2 microns in figure 17 to 6 microns in figure 46. There is, of course, a tendency for nuclear size to be correlated with cell size, but here, also, there are rather wide fluctuations. The ratio of nuclear diameter to cell diameter varies from 24.3 in figure 1 and 29.2 in figure 31 through ratios of 49.2 in figure 26 and 50.0 in figure 25 to 64.6 in figure 27 and 70.6 in figure 20. These differences are difficult to interpret but it is possible that a small individual like the one shown in figure 27 might be a nucleated fragment of a larger cell severed during the process of smearing.

2. *General Structure*—As seen in fixed and stained preparations the nucleus of *Iodamæba* is vesicular with a definite membrane, a relatively large endosome and between these the "clear zone" containing the chromatic granules disposed

upon a reticulum of fine fibrils. The appearance of the nucleus is commonly somewhat different in the cysts as compared to the trophozoites, hence it will be convenient to consider these two stages in the life cycle separately.

3. *Nuclei of Trophozoites*—In the trophozoites the organization of the nucleus is more regular and symmetrical than in the cysts. The endosome is usually a relatively large, smoothly-rounded body, central in position and in most stained preparations it appears to be homogeneous. The endosome may have other shapes and may be irregular in contour (Figs 2, 3, 18, 20, 21, 24, 25, 26, 46). In some cases the homogeneity is replaced by a variety of irregularities in its composition. There may be more lightly stained areas (Fig 65), or there may be a more deeply stained granule near the center, or there may be blocks of more deeply stained material imbedded in a more lightly stained matrix (Figs 37, 38, 43), or the more deeply stained component may appear to be reticulate (Figs 40, 41). In a few cases the more chromatic material may take the form of a peripheral layer (Fig. 45). In slides stained with hæmalum the endosome stains more lightly (Fig 65) than it does when stained with iron-hæmatoxylin.

The organization and appearance of the periendosomal layer is subject to wide variations as the accompanying illustrations show. The fundamental arrangement seems to be that of a single layer of chromatic granules rather uniformly disposed between the endosome and the nuclear membrane (Fig 65). The granules in the layer may be rather variable in size and unevenly spaced (Figs 28, 30, 33, 35). In some cases the single layer is incomplete (Figs. 2, 30, 35, 48), or the incomplete layer may become multiple on one side (Figs 3, 25, 26, 34). This change of position to one side parallels the characteristic unilateral arrangement in the cyst nucleus. The layer of granules may be close to the endosome (Figs 23, 65) or farther away (Figs. 31, 33). In some cases this layer lies against the nuclear membrane (Figs. 32, 63). The granules do not always remain distinct as such, but may show

a variety of changes. They may seem to break up into a cloud of smaller granules (Fig 66), or may become merged with the achromatic reticulum to which they are normally attached (Figs. 37, 38, 40-42). In some instances the periendosomal layer may become apparently homogeneous, lying against the endosome, either on one side (Figs. 19, 22) or surrounding it (Fig 47). In other cases the periendosomal layer seems to be absent (Fig 17). Just what becomes of the layer under such conditions is not readily explained. In some nuclei there seems to be a layer of chromatic material against the nuclear membrane in addition to the zone of granules (Figs 36, 65).

In the trophozoites from one human host there was evidence of some sort of reorganization in the nucleus. These changes are illustrated in figures 37 to 44 and the indications are that condensed masses of chromatic material form in the endosome (Figs. 37, 38, 42) and then migrate centrifugally, first out into the periendosomal layer (Figs 39-41), and then possibly out of the nucleus (Fig 44). In figure 43 the periendosomal layer is not visible and in figure 44 it seems to have become decomposed into a cloud of small granules which occupy the periphery of the periendosomal space. Figures 46 and 48 suggest changes leading to encystment, since the arrangement of periendosomal granules is unilateral as it commonly is in the cysts. Figure 47 suggests that the arrangement of the periendosomal layer just after nuclear division may be different from what it is ordinarily, and also, along with figure 68, suggests that binucleate cysts may arise by the encystment of binucleate trophozoites.

Figure 45 shows a trophozoite parasitized by *Sphaerita* and the nuclear structure appears to be degenerate. In the present instance it would be reasonable to suppose that parasitism by *Sphaerita* had been the cause of the degeneration.

4. *Nuclei of the Cysts*.—As a general rule the cysts of *Iodamæba* are uninucleate, but occasionally they may be binucleate (Figs 16, 55) and rarely a cyst may have three or possibly four nuclei (Figs. 8, 56). In figure 8 the three nuclei

could be distinguished and there was some evidence for a fourth, but the latter could not be clearly made out. In the slides from a mandrill from which figures 55 and 56 were drawn, a count of 1000 cysts gave one trinucleate and fifteen binucleate cysts.

In the cyst nucleus the endosome usually becomes displaced from the center but, in my experience, and contrary to many writers, it does not as a rule come into contact with the nuclear membrane. Occasionally such contacts are observed (Figs. 7, 60), but these nuclei are considered to be abnormal.

As in the trophozoites, the endosome is commonly homogeneous, but in some instances it may have a central granule (Figs 54, 59), or may exhibit several chromatic blocks in a matrix (Fig. 60). In figure 15 the endosome appears to be undergoing degeneration as does the nucleus as a whole.

As explained in the section on technique, the endosome of the cyst nucleus may sometimes stain more lightly than the periendosomal material.

In some sets of slides, especially those in feces that have stood for many hours to a few days, the endosome appears to diminish in size (Figs 51, 58, 61, 62). Whether this loss in volume takes place by solution or by fragmentation is difficult to determine, but there is good evidence that in some instances it is by the latter method.

There is much variation in the appearance of the periendosomal material of the cyst nuclei. While the characteristic picture is that of a crescent-shaped clump of granules on one side of the endosome, the original, more uniform disposition of the granules sometimes tends to persist after the cyst membrane has formed (Figs 5, 6, 9, 12, 13). In some cysts the crescent seems to migrate to the nuclear membrane (Fig 64), or the granules may migrate to the membrane while still in the form of a uniform layer (Figs 9, 50), or they may become secondarily scattered through the periendosomal space (Figs 51, 60, 61). In only a few cases have I seen the periendosomal material in cyst nuclei take on the appearance of a network in which the granules were indistinguishable (Fig. 57).

C. Technique

Since the study of the nuclear structure of these intestinal amoebæ is primarily limited to prepared slides, it follows that the technique used in preparing the slides is a matter of great importance. It is a well-known fact that many types of cells present different appearances with different kinds of fixatives and different kinds of stains. In the present study emphasis was placed upon the effect of different types of fixing solutions, with iron-hæmatoxylin generally employed as the stain. A few different staining methods were tried as indicated further on.

1. *Fixing Solutions*—Since Schaudinn's fluid, consisting of two parts of a saturated solution of mercuric chloride in water to one part of 95 per cent or absolute alcohol, has become so generally employed by protozoologists, especially for fixing intestinal protozoa, most of the experiments dealt with various modifications of this standard fixing fluid.

Most protozoologists add smaller or larger proportions of glacial acetic acid to Schaudinn's fluid because, as a rule, it sharpens the subsequent differentiation in staining. In these studies of *Iodamoeba* the following modifications gave essentially the same results: (1) stock solution without acetic, (2) same with 2 per cent of acetic added, (3) same with 5 per cent of acetic added, (4) one-half strength stock solution with 2 per cent or 2½ per cent of acetic added (Wenrich and Geiman, 1933). With these fixatives subsequent staining with iron-hæmatoxylin showed in normal cysts a deeply stained and homogeneous endosome with the periendosomal granules usually in a unilateral crescent, well-stained, but not so dark as the endosome.

When 10 per cent to 20 per cent of acetic acid is added to Schaudinn's fluid and the slides subsequently stained with iron-hæmatoxylin, the endosomes of cyst nuclei often stain very lightly or not at all, while the periendosomal granules appear not to be affected so that, by contrast, they are much more darkly stained than the endosomes (Figs. 54, 59). However, these effects are not uniform. In the first place,

increased amounts of acetic acid do not seem to affect the subsequent staining of the trophozoites of *Iodamoeba*. In the cysts this reversal of staining is not uniform. In some batches of slides the addition of 10 per cent of acetic serves to bring about the change (Fig. 54) while in others even 20 per cent did not produce any marked change (Fig. 12). Again, on the same slides, not all cysts show the same reaction, some will show lightly-stained endosomes while nearby cysts will have the endosomes darkly-stained, and there will be various intermediate conditions.

Other sublimate mixtures used were 95 per cent alcohol saturated with mercuric chloride without acetic and the same with 5 per cent of acetic added. In one case (human) the former gave a good fixation and subsequent staining while in another case (mandrill) the solution with 5 per cent of acetic added caused considerable distortion.

Bouin's fluid is commonly employed as a cytological and histological fixative for metazoa and it is also frequently used for fixing protozoa. Several modifications were tried in this study. With the original formula (picric, 75, formol, 25 and acetic, 5 parts) the fixation of cysts was capricious. Some cysts seemed to be satisfactorily fixed while many on the same slides were distorted and poorly stained. When this formula was modified in the proportions picric, 75, formol, 15 and acetic, 10, the fixation was generally better, although the results were not the same for all cases. The fixation of the trophozoites was better and more uniform than for the cysts. When 1 per cent of urea was added to this modified formula the results were much the same but tended to be somewhat better. In a few cases the results were excellent. When alcoholic Bouin's was tried on the cysts a great deal of distortion resulted, including the formation of protoplasmic extrusions or "buds" (Fig. 53). The staining, however, was fairly satisfactory.

Hollande's fluid, Yocum's picromercuric and Worcester's fluid all gave fair results but not so satisfactory as Schaudinn's fluid. When Carnoy-Lebrun's mixture of equal parts of alcohol, chloroform and acetic acid was used without adding

mercuric chloride the subsequent staining was very irregular. Chrom-acetic (1 per cent chromic acid, 99, acetic, 1) fixed trophozoites very well but it was not tried on cysts. Zenker's without acetic and weak Flemming's fluids gave unsatisfactory fixation for the cysts.

In general it may be said that the sublimate-alcohol-acetic mixtures, that is, Schaudinn's fluid and its modifications, are superior to the others tried for fixing the cysts. For the trophozoites a wider series of solutions gave adequate fixation.

2 *Stains*—For staining, iron-hæmatoxylin was generally employed. In a few cases saturated solution of picric acid was used for destaining. While this gave excellent results they were no better than when destaining was done with 2 per cent iron alum. Staining with ferric chloride and 1 per cent hæmatoxylin gave good results but there were no advantages over the more familiar method. Hæmalum gave the interesting result of staining the periendosomal granules intensely while the endosomes stained more lightly. These differences were not so great in the trophozoites (Fig. 65) as in the cysts (Fig. 55).

IV DISCUSSION

1. *Occurrence*—*Iodamæba butschlii* is, in my experience, the least common of the intestinal amœbæ of man. In our survey of 1060 students (Wenrich, Stabler and Arnett, 1935) the incidence, based upon one examination per student, was 1 per cent. During the past several years I have examined 640 other persons for intestinal protozoa and in this group the incidence was 2.34 per cent. These figures correspond to those obtained in other surveys in various parts of the world although Kessel and Svensson (1924) in China, Svensson (1935) in Sweden and Andrews (1934) in Mexico have reported much higher percentages in certain population groups.

The incidence of *Iodamæba* in apes and monkeys seems to be much higher than in man. Of 55 anthropoids examined 45.5 per cent harbored *Iodamæba*, but Hegner and Chu (1930) failed to find any in 44 wild monkeys examined in the Philippines. Brug (1920) was the first to record *Iodamæba* from a

monkey (*Macacus cynomolgus*) and he called it *Endolimax kueneni*. Since then, on account of the failure to find any specific differences between *Iodamæba* from man and from other anthropoids, and the successful cross infection experiments such as those of Kessel (1928), it is generally agreed that the *Iodamæba* of man and of the other anthropoids is the same species.

O'Connor (1920) first called attention to the presence of a species of *Iodamæba* in pigs and now it is known that these animals are commonly infected with this type of amœba. While natural infections of mammals other than anthropoids and pigs have not as yet been reported, Kessel (1923) and Smith (1928) were able to infect rats with *Iodamæba* from man. Recently Fantham (1932) has reported a species of *Iodamæba* from a South African tortoise and doubtless other natural hosts will be found.

2 *Nuclear Structure*—The picture of nuclear structure given in preceding pages is somewhat different from that given by many writers on *Iodamæba*. Dobell (1919) says (p. 114), "Between the karyosome and the membrane there is the usual 'clear zone,' which is occupied in the present species by a layer of fairly large granules—so-called 'peripheral chromatin'." These granules are usually in a single layer." This description seems to me to be correct and the arrangement described is fully illustrated in the drawings at the end of this paper. However, I cannot quite agree with the further statement made by Dobell that, "In ordinary iron-hæmatoxylin preparations they [the granules] are often overstained so that they are confounded with the caryosome, or they may be completely decolorized so that they disappear." It does not seem reasonable that these granules would "disappear" merely by the process of destaining. The granules may have all the hæmatoxylin extracted from them but that does not cause them to disappear. On my slides they remain visible as unstained bodies.

Except for a few cases (Fig. 57) I have not found the periendosomal material to present the foamy appearance

shown by Dobell (1919) for both trophozoites and cysts and by Taliaferro and Becker (1922) for trophozoites. Nor do I find very many instances of the clear zone being free of granules as figured by others, for example by Noller (1922).

It is true that this periendosomal layer of granules is subject to rather wide variations in appearance, as illustrated in the accompanying plates, and in some cases it is impossible to make out this layer, but these latter cases are certainly the exception to the rule. It would seem reasonable to assume. (1) that rather extensive movements may take place on the part of these granules so that they may lie either against the endosome or against the nuclear membrane, or, more commonly, in some intermediate position, (2) that the granules may become broken up into much smaller granules (Figs 44, 66), or, (3) become much less readily stainable and thus apparently merge with the net-work on which they are normally distributed (Figs 37-42). At the time of encystment these migratory tendencies are expressed in the commonly observed aggregation of the granules on one side of the endosome.

There is some evidence that the endosome itself may give off granules from its surface, or may fragment, until it is extremely difficult to see any remnant of it. This is especially true of cysts from feces that have stood for one or more days before slides are made. In such cases it is difficult to distinguish between the fragments of the endosome and the periendosomal granules themselves (Fig 61).

In figures 37 to 44 evidence is presented indicating some sort of reorganization of the nuclear structure, especially the endosome. It is, of course, impossible to say whether these changes represent a normal process or a degenerative one. Some conditions are interpreted as definitely degenerative, such as the migration of the endosome to the nuclear membrane (Figs 7, 45). In figure 15 the nucleus appears to be breaking down. The condensation of the nucleus into a sac-like condition as shown in figure 60 is also regarded as a sign of degeneration.

The appearance and behavior of the periendosomal

granules suggest that they constitute the chromosomal chromatin. Hence, when details of nuclear division come to be worked out, it would be expected that the chromosomes should form out of these granules. Reichenow (1929, p. 734) states that these granules gave a positive nucleal reaction, and this, together with their retention of the stain when stained by hæmatoxylin or hæmalum and when the endosome tends to lose its stain, would tend to support this idea.

3. *Chromatoidal Material*—Dobell (1919) noted round bodies of volutin-like material in the cysts of *Iodamæba*, but did not mention any chromatoidal material. Definite chromatoid bodies, such as those commonly found in the cysts of *Endamæba histolytica* and *E. coli*, have not, so far as I am aware, been recognized for *Iodamæba* although Brug (1920) noticed darker areas in the cytoplasm of the cysts of his "*Endolimax kueneni*" from a monkey. When the present study was first begun it was noted that in stained slides the cytoplasm immediately surrounding the glycogen vacuole was often very darkly stained. Taliaferro and Becker (1922) show this darkened border of the vacuole in their figure 10. Since chromatoids are often seen to be crowded around the glycogen area in the cysts of species of *Endamæba*, especially *E. coli*, it seems reasonable that there might be chromatoidal material in a diffused state in these darker areas of *Iodamæba*. If chromatoidal material is present, it might form into definite bodies in some cases or remain diffuse in others. This is the interpretation that I have placed upon the deeply stained material in the cysts of *Iodamæba*. As previously noted, darkened borders of glycogen areas are seen in figures 4, 7, 8 and 13 and more definite bodies are seen in figures 49, 51, 52 and 60. The paired condition of these bodies in figure 52 recalls the frequently paired condition of chromatoids in the cysts of *E. histolytica* as noted by Hegner and Chu (1930). In addition to the chromatoidal material just mentioned, various round volutin-like granules are to be seen, as noted by Dobell (1919).

4. *Technique*—There are extensive possibilities for experi-

mentation by the use of different technical methods in the preparation of stained slides. In the present study I have contented myself with trying some of the more common fixatives and modifications of them and I have conducted relatively few experiments on the use of different stains.

It is interesting to note that the endosomes of the cysts tend to lose their stainability with iron-hæmatoxylin when from 10 per cent to 20 per cent of acetic acid is added to Schaudinn's fluid, just as Stabler (1932) has shown to be true of *Endolimax nana*, especially for the trophozoites of that species. The increased amount of acetic acid in this fixative does not seem to affect the periendosomal granules nor does it seem to affect the endosomes of the trophozoites. It is also interesting that this change or reversal in stainability is not uniform for the cysts either for all cases of *Iodamæba* or even, sometimes, for the same case.

In my experience Bouin's fluid and its modifications, while apparently giving a satisfactory fixation for the trophozoites of the intestinal amœbæ, are not usually so satisfactory for the cysts. The evidence indicates that these combinations do not penetrate the cyst membrane as readily as do the sublimate-alcohol-acetic mixtures.

Alcoholic Bouin's fluid produced a good deal of distortion of the cysts of *Iodamæba* including the formation of "buds" comparable to those claimed to be characteristic for the genus "*Councilmania*" by Kofoid and his associates (1921, 1923, 1927, 1928). Gunn (1922), Wight and Prince (1927), Segal (1928), Freeman (1929) and Stabler (1932a) have shown that such "buds" are artifacts produced by various physical and chemical agents. Wight and Prince show photographs of cysts of *Iodamæba* with "buds" produced by hot Schaudinn's fluid. Freeman, Segal and Stabler found that picromercuric solution was one of the most effective agents in producing "buds" on *Endolimax nana* and *Endamæba coli*. In these experiments on *Iodamæba*, picromercuric very seldom produced "buds" but the alcoholic Bouin's produced more of them.

It is interesting to note that hæmalum does not stain the endosome of *Iodamæba* as heavily as does iron-hæmatoxylin, but does stain the periendosomal granules very well. The only time that we tried the Feulgen method only negative results were obtained. However, Reichenow (1929) states that the periendosomal granules gave a positive nucleal reaction.

5 *Relation of Iodamæba to Other Amœbæ*—The true relationships between *Iodamæba* and other amœbæ cannot be determined until its life history has been more completely worked out. In a superficial way the nuclear structure shows resemblances to that of such organisms as *Vahlkampfia tachypodia*, *Cochliopodium bilimbosum*, *Hartmanella lamellipodia* or species of *Amphizonella* (see Noller, 1922), but until the role of the endosome and of the periendosomal zone in the process of nuclear division is determined one cannot know how close these relationships really are. There is a certain degree of resemblance between the nuclear structure of *Iodamæba* and that of *Dientamæba*. The latter species, however, has a very small endosome which is usually eccentric and which may not be much larger than the periendosomal granules with which it is associated in a common matrix (Wenrich, 1936).

When the periendosomal granules of the nucleus of *Iodamæba* come to lie against the nuclear membrane, the resulting appearance is similar to that of the nucleus of *Endolimax nana* when the peripheral granules of that species are clearly visible. Since, however, in most cases, and with the more commonly employed techniques, the peripheral granules of the nucleus of *Endolimax* are not readily seen, this more common appearance can be confused with that of the nuclei of *Iodamæba* in which the periendosomal granules are apparently absent. Some of the small individuals of *Iodamæba* in the case from which figures 17 to 26 were made, could easily be mistaken for specimens of *Endolimax nana*. In a few cases there are whole infections of small trophozoite amœbæ which are extremely difficult to diagnose as between

Endolimax nana and small specimens of *Iodamæba*. A combination of a peripheral position for the periendosomal granules of *Iodamæba* with a small endosome would produce pictures closely similar to those of the nuclei of the species of *Endamæba*. Fortunately, *Iodamæba* in its typical condition is sufficiently distinct from other species that little confusion need arise. Extreme variants, however, are likely to be disturbing to the diagnostician. The chief problem yet to be worked out in connection with *Iodamæba* is its complete life history, with special emphasis upon the process of nuclear division.

V. SUMMARY

Iodamæba butschlii was found in 26 out of 1700 human hosts examined and in 25 out of 55 apes and monkeys examined.

Measurements of trophozoites, when made from slides fixed in Schaudinn's fluid gave a range of diameter from 4 to 19 microns with averages for three different hosts as follows (1) 10.60, (2) 11.27 and (3) 5.58 microns. From a slide of case 2, fixed in modified Bouin's fluid, the average was 13.51, indicating less shrinkage than for Schaudinn's fluid. The small size in case 3 suggests a small race. Trophozoites from two chimpanzees gave average diameters of 11.70 and 11.03 microns.

Measurements of cysts gave ranges of diameters from 7 to 13 microns with averages of 10.23, 10.11 and 7.94 microns for the three human hosts.

As seen in fixed and stained slides the nucleus is vesicular in structure with a definite membrane, a relatively large endosome and in the space between these a layer of granules disposed on a fine fibrous network.

Although the endosome is usually smoothly rounded and homogeneous, it presents many variations including irregular shapes and a heterogeneous constitution. The endosome apparently may sometimes give off fragments to the surrounding "clear zone." In the cysts the endosome tends to become eccentric but does not normally rest against the nuclear membrane.

The periendosomal granules vary in position from contact with the endosome to contact with the nuclear membrane, although normally occupying an intermediate position. The single layer may become incomplete, or restricted to one side, especially in the cysts. In this unilateral arrangement the layer tends to become multiple. In some cases the granules become resolved into a cloud of smaller granules or may seem to become merged into the reticulum upon which they normally rest. In some cases the granules seem to be absent.

Of various fixing solutions tried, Schaudinn's fluid with small amounts (up to 5 per cent) of glacial acetic acid added seemed to give the best results. When 10 per cent to 20 per cent of acetic was added, the endosomes of the cyst nuclei tended to lose stainability, while the periendosomal granules were unaffected, or stained more deeply. In the trophozoites the endosomes did not show this loss of stainability. Bouin's fluid and some of its modifications are satisfactory for trophozoites but are not so useful for cysts. Alcoholic Bouin's caused protoplasmic extrusions or "buds" to form on the cysts. Hæmalum did not stain the endosome as deeply as did iron-hæmatoxylin. This lack of stainability was more marked in the cysts than in the trophozoites.

In addition to volutin-like granules in the cysts, described by Dobell and others, there is commonly some chromatoidal material which shows as more deeply staining areas or streaks against the glycogen vacuole or may appear in more or less definitely formed bodies or masses.

The relationships of *Iodamæba* with other amœbæ cannot be determined until its life history, especially the process of nuclear division, has been worked out.

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VII EXPLANATION OF FIGURES

All figures have been made with the aid of a camera lucida at an initial magnification of $\times 3000$. In printing they have been reduced about one-fourth. Unless otherwise stated they are made from slides fixed in Schaudinn's fluid plus 5 per cent of acetic acid and stained with iron-haematoxylin.

PLATE I

All the figures on this plate were drawn by Mr R. L. Brown from slides of a single infection (man).

FIGS 1-3, trophozoites

FIG 1 Typical individual, nucleus with large deeply-stained endosome surrounded by a row of granules attached to it by radial fibrils

FIG 2 Small individual with larger nucleus, endosome elongated, granular ring not quite complete

FIG 3 Probably precystic individual, food bodies mostly absent, endosome of nucleus relatively small, granules more numerous on one side of endosome

FIG 4 Large early cyst. Large nucleus with granules still in a ring around endosome, apparently several glycogen vacuoles not yet coalesced, dark chromatoidal strands at periphery of glycogen vacuoles

FIG 5 Cyst of irregular contour, granules of perienosomal ring uneven in size

FIG 6 Normal-sized cyst, note volutin-like granules in cytoplasm, one large intranuclear granule attached to endosome

FIG 7 Cyst with small nucleus, endosome a lateral plaque against the nuclear membrane, an unusual condition considered to be abnormal

FIG 8 Round cyst with three and possibly four nuclei, fourth nucleus not clearly distinguishable

FIG 9 Large cyst with perienosomal granules of nucleus arranged as a peripheral ring as in species of *Endamaba*

FIGS 10-16 Cysts from slides fixed in Schaudinn's plus 20 per cent of acetic acid

FIGS 10 and 11 Cysts with lightly staining endosomes in nuclei, granules massed into crescents

FIG 12 Large cyst with endosome of nucleus staining more darkly, granules not confined to a lateral crescent

FIG 13 Smaller cyst, small endosome in nucleus, granules not confined to a crescent

FIG 14 Cyst with lightly stained endosome in nucleus, most of granules in a crescent

FIG 15 Cyst with degenerate nucleus, nuclear membrane apparently breaking down

FIG. 16 Binucleate cyst; small, more lightly stained endosomes, granules in well-defined crescents

PLATE II

All figures on this plate drawn by Mr R. L. Brown from slides fixed in Schaudinn's fluid plus 5 per cent of acetic

FIGS 17-26 Small trophozoites possibly representing a small race (cf Fig 62 of cyst)

- FIG 17 Small individual, 4μ in diam, periosomal granules not discernible
- FIG 18. Slightly larger individual, endosome irregular in contour.
- FIG 19 Individual with more homogeneous cytoplasm (precystic?), a few periosomal granules at left of endosome
- FIG 20 Small individual with relatively very large nucleus, endosome small, large crescent of periosomal granules
- FIG 21. Larger individual ($7\mu \times 8\mu$) with small nucleus; endosome irregular in contour, granules partly shifted to one side
- FIG 22 Individual with larger nucleus, periosomal crescent in close contact with endosome
- FIG 23 Individual with normal nucleus, periosomal granules form a ring
- FIGS 24-26 Larger individuals with enlarged nuclei, misshapen endosomes and lateral disposition of granules—possibly degenerate, or precystic
- FIGS 27-36 Trophozoites from a chimpanzee which had just arrived from Africa
- FIG 27 Unusually small individual with exceptionally large nucleus, layer of granules not very distinct
- FIG 28 Small individual with irregular endosome in nucleus; layer of granules uneven
- FIG 29 Typical individual with complete ring of granules around the endosome of the nucleus
- FIG 30 Somewhat larger individual, endosome of nucleus irregular in shape, ring of granules incomplete
- FIG 31 Typical individual, ring of granules in nucleus close to membrane
- FIG 32 Individual showing ring of granules against the nuclear membrane
- FIG 33 Individual showing periosomal granules irregular in size and arrangement
- FIGS 34 and 35 Individuals showing nuclear granules shifted to one side of endosome
- FIG 36 Large individual ($20\mu \times 16\mu$), nucleus fairly typical, some peripheral chromatic material against the nuclear membrane on the right

PLATE III

All figures from one human case Figures 43-45 and 47 from slides fixed in Schaudinn's fluid plus 5 per cent of acetic acid, all others from slide fixed in modified Bouin's fluid

FIGS 37 and 38 Individuals showing heterogeneous endosomes; granules of periosomal layer indistinct.

FIGS 39, 40, and 41 Individuals showing deeply-stained granules in the less deeply-stained periosomal ring, possibly having emerged from the endosome Figure 41 shows an ingested *Blastocystis*

FIG. 42 Individual showing deeply stained mass at edge of endosome as if ready to emerge

FIG 43 Individual showing misshapen nucleus, periosomal layer not discernible, deeply-stained granule at one side in a lobe of the nucleus

FIG 44. Individual showing deeply-stained granule apparently emerging from the nucleus, a cloud of finer granules in outer nuclear zone

FIG 45. Individual parasitized by *Sphaeria*, endosome at one pole of nucleus, granules at other pole; probably abnormal

FIG. 46 Individual with hypertrophied nucleus, enlarged endosome with irregular contour and granules in a crescent

FIG 47. Binucleate individual with periosomal layers as homogeneous zones against the endosomes

FIG 48 Large individual with incomplete ring of granules (precystic?)

PLATE IV

FIGS 49-51 Cysts from one human host

FIG 49 Typical cyst with somewhat eccentric endosome, lateral grouping of granules, glycogen vacuole and irregular chromatoid mass

FIG 50 Cyst with periendosomal granules distributed against the nuclear membrane

FIG 51 Large cyst with granules scattered irregularly through the nuclear space, irregular chromatoid strand

FIG 52 Cyst from another human host with long paired chromatoids

FIG 53 Cyst from mandrill showing a "bud", from slide fixed with alcoholic Bouin's fluid

FIG 54 Cyst from man, 2 days old, fixed with Schaudinn's with 10 per cent of acetic, endosome lightly stained and with central granule

FIG 55 Binucleate cyst from mandrill; hæmalum staining, faintly stained endosomes

FIG 56 Trinucleate cyst from mandrill (same host as for Figs 53 and 55) Note heavily-stained endosomes

FIG 57 Cyst from anubis baboon, nucleus with periendosomal material in form of network, as shown by certain authors (1/2 strength Schaudinn's plus 2 per cent of acetic)

FIGS 58 and 59 Cysts from same set of slides (Man)

FIG 58 From slide fixed in Schaudinn's plus 5 per cent of acetic, note darkly-stained endosome

FIG 59 From slide fixed in Schaudinn's plus 20 per cent of acetic, note faintly-stained endosome

FIG 60 Cyst with sac-like nucleus as seen in older specimens, endosome partly broken up, large chromatoid mass (Man)

FIG 61 Cyst with nucleus showing small endosome surrounded by an augmented number of granules (Man)

FIG 62 Small cyst from host with "small race" (cf Figs 17-26)

FIGS 63 and 64 Small trophozoite and small cyst from another human host having mostly normal-sized amoebæ (Cf Figs 1-16)

FIGS 65-67 Trophozoites from same chimpanzee

FIG 65 From slide stained in hæmalum, note lightly stained endosome and layer of chromatic material against the nuclear membrane

FIG 66 Iron-hæmatoxylin stain, note peripheral zone of very fine granules

FIG 67 Two endosomes in nucleus, suggesting some stage of division

FIG 68 Binucleate trophozoite from another chimpanzee Binucleate cysts may come from such trophozoites

PLATE I



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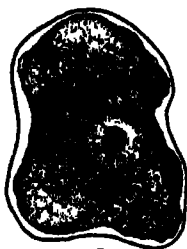
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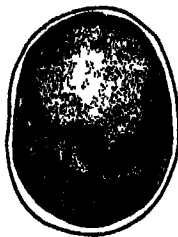
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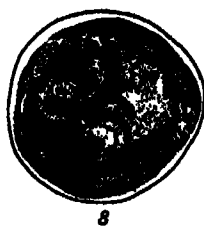
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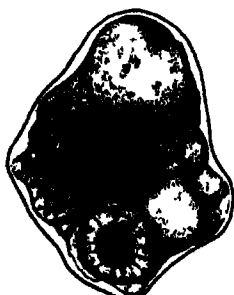
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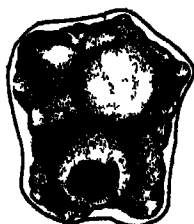
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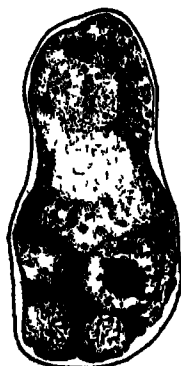
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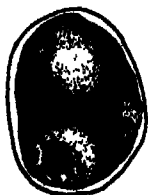
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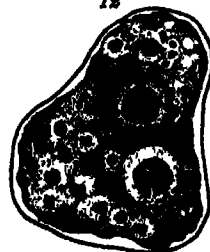
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PLATE II



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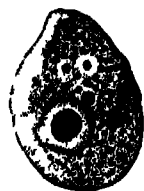
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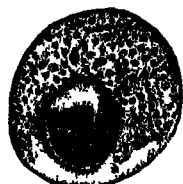
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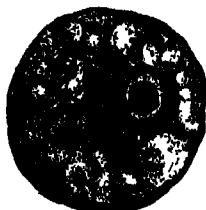
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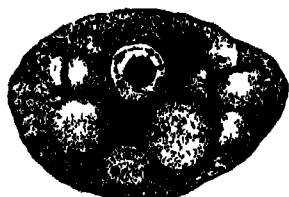
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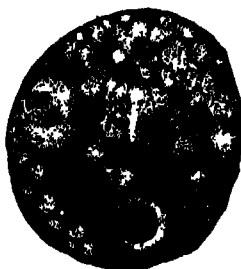
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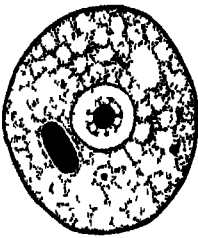


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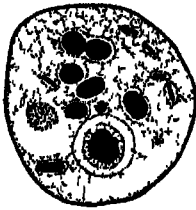


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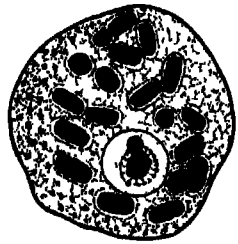
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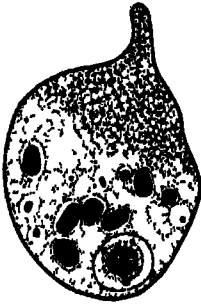
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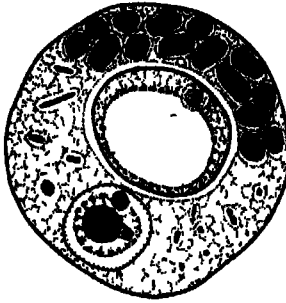
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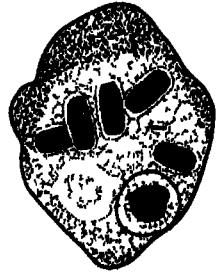
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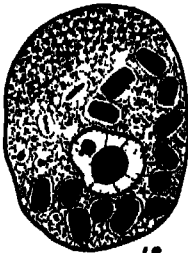
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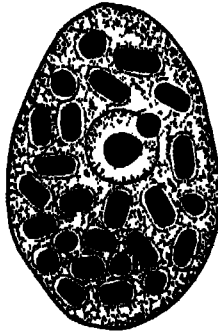
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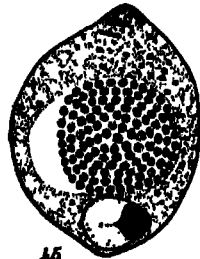
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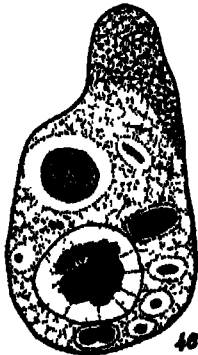
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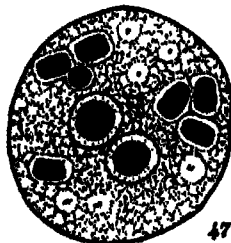
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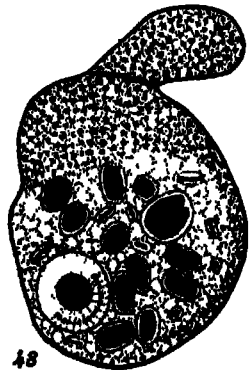
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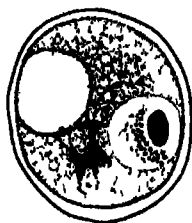


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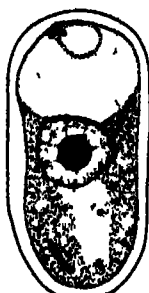


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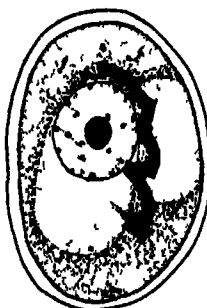
PLATE IV



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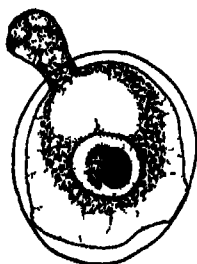
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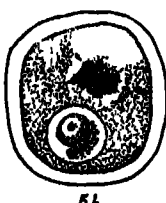
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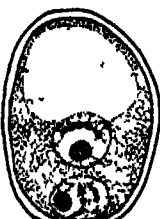
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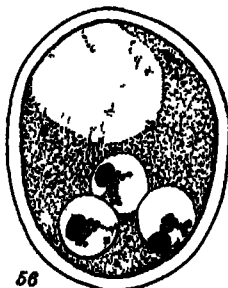
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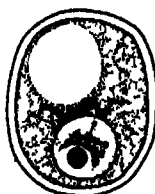
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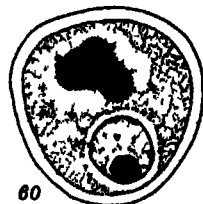
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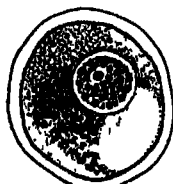
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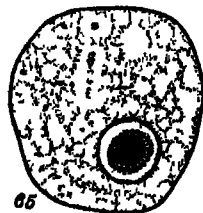
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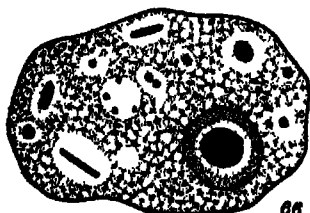
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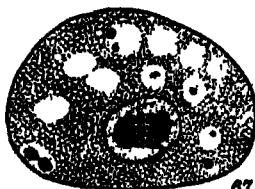
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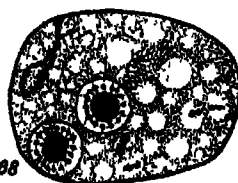
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THE CONTINUITY OF STRUCTURE AND FUNCTION IN THE NEUROMOTOR SYSTEM OF EUPLOTES PATELLA DURING ITS LIFE CYCLE

DATUS M. HAMMOND AND CHARLES A. KOFOID

(Read April 23, 1936)

ABSTRACT

The nuclear aspects of binary fission and conjugation have been worked out in many ciliates, but for relatively few cases is there detailed knowledge of the cytoplasmic changes during these stages of the life cycle. The possession of a complicated neuromotor system makes *Euplotes patella* ideal material for a study of this kind. This neuromotor system undergoes a process of reorganization of structure at certain definite intervals in the life cycle. Such a process occurs at each binary fission, and during conjugation there are two reorganizations of the neuromotor system. The first of these takes place during the maturation divisions preparatory to fertilization, and the second occurs during the differentiation of the nuclei following fertilization. During these reorganizations certain structures, including the cirri with their fibrils, and the peripheral polygonal system, undergo dedifferentiation and redifferentiation, while in others, including the peristome and bristles, no change of structure could be detected. In the reorganizations during conjugation, however, there is a replacement of the old peristome, and thus these reorganizations, coincident with the ending of one life cycle and the beginning of another, are more profound than that occurring at binary fission. In spite of the change in structure at these times the functional continuity of the neuromotor system is maintained throughout the life cycle.

THE life cycle of the ciliate Protozoa presents certain unique aspects which concern basic biological concepts of wide application and also certain unusual modifications of these. They are as follows: (1) The ciliate protozoan, from the standpoint of nuclei, is multicellular. (2) The differentiation of sex and somatic cells occurs (in *Paramecium*) in the eight-cell cleavage stage of the somatella following the third cleavage mitosis. (3) The surviving pronucleus inherits as a one-celled haploid organism the entire differentiated body of its diploid binucleate ancestor. (4) A single asexual fission of this pronucleus results in a resident and a migrant gamete with very unequal amounts of cytoplasm. (5) The resulting zygotes or exconjugants complete the resorption of the somatic nucleus of their diploid ancestor. (6) Throughout the entire process of maturation, fertilization, and cleavage

the complicated, highly differentiated ciliary mechanism is maintained sufficiently intact and active to provide for the coordinated activity of its several parts and orderly locomotion, there being at no time a complete return to a de-differentiated condition comparable to that of the fertilized egg of the metazoan (7) During binary fission, in which both sexual and somatic nuclei divide, two completed individuals result, and throughout the process coordinated locomotor activities continue

During this life cycle there is a succession of individuals functioning under differing nuclear and changing cytoplasmic control. The zygote as a one-celled organism initiates the new genetic or Huxleyan individual which grows to an eight-celled somatella. By degeneration of three of four sex nuclei and two divisions of the survivor, accompanied by the binary fissions which distribute the four somatic nuclei, the cycle is carried through the period of adolescence. There result four fully differentiated adults now capable of sexual reproduction, and generally going through repeated binary fissions of this adult stage.

The concept of a structurally integrated neuromotor system by which the complex activities of the ciliate are coordinated was developed under the direction of the senior author by Sharp (1914), who first described in detail this integrated fibrillar system in the ophryoscolecoid ciliate *Diplodinium* from the stomach of the ox. A series of papers from this laboratory published in the University of California Publications in Zoology and elsewhere by investigators trained here has confirmed the existence of this system in other families of ciliates and elaborated the details of its modifications. Some European protozoologists have ascribed to the neuromotor system merely a supporting function, regardless of the fact that its integration is always with all motor organelles and without evident relation to the support of the body as a whole. ¶

The purpose of this investigation is to trace the progress of this fibrillar system through the succession of functional

individuals constituting the changing panorama of the life cycle of the ciliate protozoan. Added interest attaches to this succession because of the fact that coördinated locomotion is at no instant suspended or lacking in the individual at whatever stage of the cycle it exists. This continuity of coordination crosses the biologically significant gaps which separate the diploid-haploid-diploid succession in maturation and fertilization, persists through the prolonged stage of conjugation in which two conjugants maintain intimate protoplasmic connection and interchange migrant nuclei, and is maintained during transverse fission and the processes of reorganization resulting in the formation of two mature bodies out of one. This continuity makes an investigation of the specific changes in the coordinating mechanism in relation to the processes of dedifferentiation and redifferentiation both opportune and significant.

Dedifferentiation in addition to redifferentiation of organelles at the time of binary fission was first noticed in the ciliates by Stein (1859). Engelmann (1862) found that this reorganization process also occurred at the time of conjugation. Maupas (1889) extended the observations of Engelmann. In some hypotrichous ciliates he found two more or less complete replacements of organelles, or "moult," as he called them, during the course of conjugation. These interesting phenomena have received no satisfactory explanation. In 1923 Kofoid advanced the viewpoint that the Protozoa go through a life cycle which is comparable to that of Metazoa. This life cycle begins with the zygote, which undergoes successive periods of cleavage, differentiation, asexual reproduction, senescence and finally death. This conception thus afforded a new approach to the study of the reorganization of protoplasmic structure during sexual and asexual reproduction.

STRUCTURE

The fresh-water ciliate *Euplotes patella* is one of the most complex members of the group Hypotricha. In order to make clear the description of the changes in structure during

asexual and sexual reproduction, a brief account of its morphology will be given.

The organism averages 150 x 90 microns in dimensions. It is shaped somewhat like a limpet, with an arched dorsal surface and a more or less flat ventral surface, which is hollowed out in the left anterior region to form the peristome. This peristomial field is bounded anteriorly and on the left by a spiral adoral zone of membranelles, leading into the cytopharynx (Pl. 1, memb) The organelles of locomotion consist of eighteen cirri, each formed of clustered fused cilia, distributed over the ventral surface According to position these cirri are termed frontal, ventral, anal, and marginal (fr cir, etc) The most highly developed are the anal cirri, which are coordinated in action with the adoral zone of membranelles by means of an integrated system of neuromotor fibrils These were described as a neuromotor system by Yocom (1918) and their neuroid function was demonstrated experimentally by Taylor (1920)

The basal granules of the constituent cilia of each cirrus are arranged in definite, straight, obliquely directed rows, and fibrils radiating from the bases of the cirri are oriented in general with respect to these rows This arrangement we interpret as indicating the evolution of the organism from an ancestor with a simple neuromotor system in which the cilia were uniformly distributed over the surface of the body in longitudinal, slightly spiral rows, as in the primitive holotrichous ciliates. The clustered cilia of each cirrus thus represent a given area of the ancestral pattern, and the radiating fibrils represent in their orientation both the longitudinal ciliary lines and the transverse commissures between them.

On the dorsal surface there are no cirri, but the ancestral ciliation is represented by nine longitudinal rows of short, seta-like bristles (Pl 3, dor. br.). An additional row is present on the left ventral surface (Pl. 1, vent. br.). Each bristle has a complex basal apparatus consisting of a basal granule lying in a funnel-shaped depression, surrounded by a

group of rodlets arranged in the manner of a rosette. Groups of rodlets also occur at the bases of the membranelles and cirri. The bristles are linked together by a network of pellicular lines forming the peripheral polygonal, or so-called silverline system, which extends on both dorsal and ventral surfaces. This system, first described for *E. patella* by Turner (1933), covers the entire surface of the body with a pattern of regular polygons on the dorsal surface and of irregular polygons on the ventral surface. The bristles represent modifications of the dorsal cilia of the ancestral form and are interpreted as sensory structures.

The organism has a macronucleus shaped like the figure 3, and a compact micronucleus located in the left anterior corner of the macronucleus.

THE NEUROMOTOR SYSTEM IN ASEQUAL REPRODUCTION

During asexual reproduction by transverse fission the macronucleus undergoes a process of progressive reorganization beginning at each end and progressing toward the center (Pl. 2, reorg. ban.). The micronucleus divides mitotically and each daughter receives a product of this division, as well as half of the reorganized macronucleus.

These nuclear phenomena are accompanied by extensive changes in the cytoplasmic structures, mainly in the neuromotor system. Transverse fission necessitates the development of new posterior parts, including cirri, bristles, and polygonal system for the anterior daughter, and new anterior parts, including peristome, cirri, bristles, and polygonal system for the posterior daughter. To take the place of the one previously present, two complete neuromotor systems are developed by several methods in different parts of the system. The first method involves the retention without modification of old structures, and the development of new ones to make two complete sets of the structures in question. This is of necessity diversely carried out in the two daughters. The old peristome with its adoral zone of membranelles is retained in entirety without any visible change in structure.

by the anterior daughter, while a new peristome is developed independently for the posterior daughter, with no apparent fibrillar connection with the old structure but arising very close to it (Pl 2, an per post). The anterior bristles in each row are retained unmodified by the anterior daughter, and the posterior bristles by the posterior daughter. Supplementary bristles are developed by a series of fissions of the basal granules in a region on each side of the future plane of constriction which parts the daughters (Pl 2, reg mult. br). A similar process of multiplication of the bristles was described by Gelei (1934) in an undetermined species of *Euplotes*. There is apparently a gradient of regenerative activity present, with its highest level at the future plane of constriction, and decreasing both anteriorly and posteriorly in each line of bristles. Only those basal granules of the bristles near the center of each row are involved in the process of multiplication, the basal granules nearest the future plane of constriction begin fission earlier and produce more daughter granules than those farther from this plane.

The old peristome and bristles are thus passed on from the parent organism to the daughters without any detectable change of structure. This does not support the idea advanced by Taylor (1935) that there is a complete dedifferentiation of the Protozoan body at each binary fission.

A feature of interest in connection with the development of the bristles is the differentiation of certain of the cirri along the rows of bristles on the dorsal surface. The anlagen of the two right marginal cirri for the anterior daughter arise near the center of the region of multiplication of the last two rows of bristles to the right, and those for the posterior daughter appear in the same two rows near the posterior end. These anlagen increase in size, and at the time of the separation of the two daughters the cirri assume their definitive positions on the ventral surface. The differentiation of these cirri in such close connection with the bristles is an indication that the cirri and bristles are related phylogenetically.

Another method of developing new parts of the neuromotor

system involves a complete replacement of structure, i.e., a complete rejuvenescence. The one entire set of old structures, for example, the cirri and the neuromotor fibrils attached to these, is dedifferentiated and two new sets, one for each of the daughters, are redifferentiated in new locations (Pl. 2). The cirri and their fibrils are therefore entirely renewed at each asexual reproduction. This also holds true for the entire polygonal system, new networks of which are differentiated at the time when the anlagen of the new cirri, bristles, and peristome are developing. These new networks originate in many separate loci surrounding the other neuromotor anlagen and are fully formed in miniature at the time when the network is first visible. Development occurs by coincident expansion of these areas, by which the pattern of this network is retained. The old polygonal system is dedifferentiated as the new networks expand, and this process continues until the new networks come together and fuse, without trace of a suture, to form an integrated new polygonal system covering the entire surface of the body, with the possible exception of the old peristomial field. Replacement in the old peristomial field may not occur at all, since the old membranelle zone is not replaced. The development of a new peristomial network would be expected to arise in connection with a membranelle zone.

The gradient of regenerative activity is also seen in the development of the cirri, since all eighteen cirri for each daughter, with the exception of the two right marginal cirri for the posterior daughter, arise near the future plane of constriction and later move to their definitive positions (Pl. 2). The new peristome and the whole of the new polygonal system, except the portions arising on the extreme anterior end of the anterior daughter and on the posterior end of the posterior daughter, originate in this locality of general dedifferentiation and redifferentiation.

The anterior daughter retains the old peristome with its polygonal system, its large adoral zone of membranelles, and a number of old bristles in its anterior part. It develops

anew the entire set of eighteen cirri, the neuromotor fibrils attached to these, the polygonal system over the entire surface of the body other than the peristomial field, and a number of bristles in its posterior region.

The posterior daughter retains a number of old bristles in its posterior region, but the remaining parts of the neuromotor system, including the anterior bristles, the peristome, the eighteen cirri, and the polygonal system, are formed anew upon it. All of these parts with the exception of the bristles arise *de novo*

THE NEUROMOTOR SYSTEM IN SEXUAL REPRODUCTION

The nuclear phases of conjugation have been described by Turner (1930). According to his description the micronucleus of each conjugant undergoes four successive divisions, the middle two of which are meiotic. Of the eight haploid products of the first three divisions six degenerate, two divide again, and of the four products two degenerate and the remaining two become, respectively, the resident and migrant pronuclei.

These migrant pronuclei are mutually exchanged between the conjugants, and fertilization results. In each conjugant the macronucleus breaks up and degenerates. Remnants are present until the beginning of the first binary fission of the exconjugant. Turner's (1930) conclusion that a part of the old macronucleus fuses with and becomes a part of the new macronucleus requires confirmation. The zygote nucleus of each conjugant undergoes two "cleavage" divisions, and two of the resulting nuclei form, respectively, a new micronucleus and macronucleus, while the other two nuclei degenerate. Thus, during these processes the organism is successively diploid with the parental neuromotor system, haploid with that of the gamete, and again diploid with that of the zygote.

With respect to cytoplasmic reorganization these stages of sexual reproduction differ from asexual reproduction in that only one neuromotor system is redifferentiated in each gamete instead of two, as in the prospective schizont at binary fission,

and, further, in that the reorganized neuromotor system of the gamete is immediately replaced by a second single reorganized system of the zygote

REORGANIZATION OF THE GAMETE

Soon after two organisms have come together in conjugation and during the approach of meiosis the posterior part of the adoral zone of each conjugant is drawn into the endoplasm, where it is slowly dedifferentiated and resorbed (Pl 3, rem memb.) During the meiotic divisions of the micronucleus the anterior part of a new adoral zone appears, and replaces the remnant of the old adoral zone (an ant memb) Since the posterior portion is not included in the newly differentiated structure, the adoral zone is still incomplete after the replacement Soon after the appearance of this anlage, the anlages of a new set of cirri and their fibrils arise in the positions characteristic of the corresponding anlages for the posterior daughter during binary fission (Pl 3) Frontal cirrus 4, which at all other reorganizations arises in the peristomial field, fails to appear in the set differentiated during gametic reorganization Thus, when replacement has been completed the organism has only 17 instead of 18 cirri No evidence of dedifferentiation or redifferentiation of the bristles or of the peripheral polygonal system on the dorsal surface was seen during either meiosis or fertilization There is, however, some evidence of a replacement of the polygonal system on the whole ventral surface similar to that which occurs in binary fission.

The first reorganization of the neuromotor system begins during the meiotic processes preparatory to fertilization and therefore is called collectively the reorganization of the gamete. However, the replacement of the old set of cirri, fibrils of the cirri, and the anterior portion of the adoral zone is not completed until after fertilization and the separation of the conjugants have occurred The exconjugants, possessing the cytoplasmic structures differentiated during the stage of the gamete, are thus characterized by having each

an incomplete set of cirri and an incomplete peristome. The posterior portion of the peristome, including the cytopharynx and its ciliary apparatus, is entirely lacking. Ingestion of food cannot occur while this condition persists.

REORGANIZATION OF THE ZYGOTE

Cleavage and differentiation of the macronucleus and micronucleus in the exconjugant require about two days, a relatively long period of time. One of the cleavage nuclei gradually increases in size, and about two days after the separation of the conjugants it begins to elongate laterally. At about this time the second complete reorganization of the neuromotor system occurs. Since this takes place in the new genetic individual developing from the zygote it is termed the reorganization of the zygote.

During this reorganization the incomplete set of cirri and their fibrils, differentiated during the stage of the gamete, is entirely replaced by a complete new set arising in a similar manner. The incomplete peristome of the gamete is now made complete by the addition of the posterior portion, which develops from an anlage arising immediately posterior to the incomplete adoral zone.

When the reorganization of the zygote is finished the organism has a complete neuromotor system similar to that of the parent. The first binary fission after conjugation occurs in the usual manner with regard to the neuromotor system.

In the individual resulting from the reorganization of the gamete the bristles and dorsal peripheral polygonal system are retained without visible change of structure from that of the parental organization. The cirri and their fibrils, the anterior portion of the peristome, and presumably the ventral polygonal system are redifferentiated, while the corresponding structures of the old organization, including the entire peristome and its adoral zone of membranelles are resorbed.

After the reorganization of the zygote the new genetic individual begins its life cycle with the bristles and dorsal

peripheral polygonal system carried over from the pre-gametic individual. The anterior portion of the peristome is carried over from the gametic individual. The posterior portion of the peristome with the remainder of the adoral zone and the cirri with their fibrils are redifferentiated in the reorganization of the zygote.

SUMMARY

The neuromotor system of *Euplotes patella* is continuous throughout its life cycle in the sense that functional activity is maintained at all times. This is accomplished, first, by the retention of certain parts of the system from one functional individual to the next, and, second, by the overlapping in time of the dedifferentiation of the remaining portions of the neuromotor system and the redifferentiation of the corresponding structures in the new system. There is no complete dedifferentiation of the entire system at any one time, neither in the gamete nor the zygote. It is possible that surviving parts not dedifferentiated at these critical moments in the cycle are subsequently slowly replaced, but no evidence of such general and complete reorganization has been found.

It is significant that the most far-reaching reorganizations of the neuromotor system occur at the time of the major cyclic changes, as when functional individuals with new nuclear control, such as the gamete and zygote, arrive in the cycle. Thus during the reorganization of the gamete only seventeen cirri are redifferentiated instead of the usual eighteen. An inspection of the sequence of changes in the neuromotor system reveals a significant adaptive aspect to the need of a functioning individual in the continuity of a mechanism adequate for use in locomotion and available for feeding when this is continued or resumed. Logically, if senescence is the physiological occasion for dedifferentiation, this process should not be partial but complete. Utility rather than logic thus seems to preside over the succession of complex series of dedifferentiations, redifferentiations, supplemental additions, and temporary dropping out of the fibrillar elements which

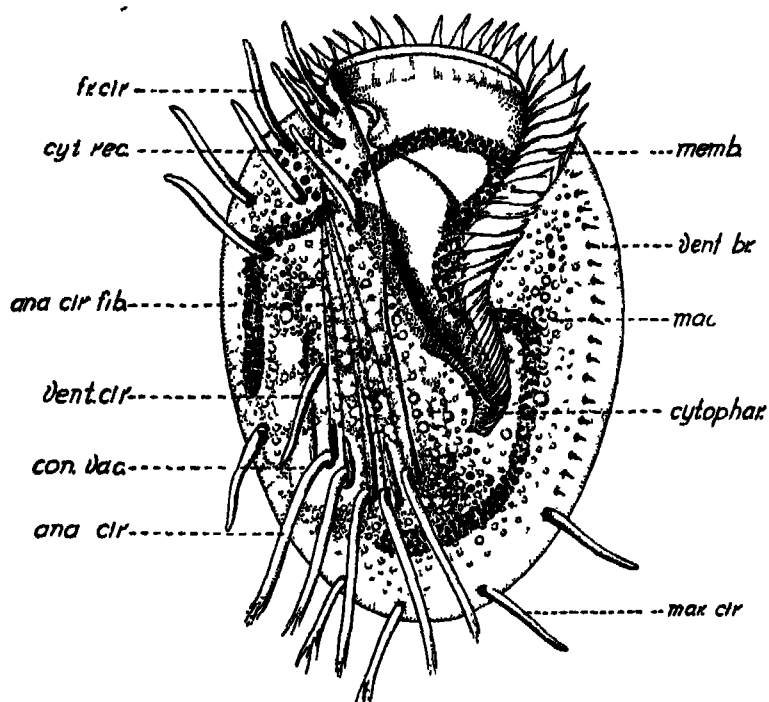
constitute the structurally integrated neuromotor system of *Euplores*.

DEPARTMENT OF ZOOLOGY,
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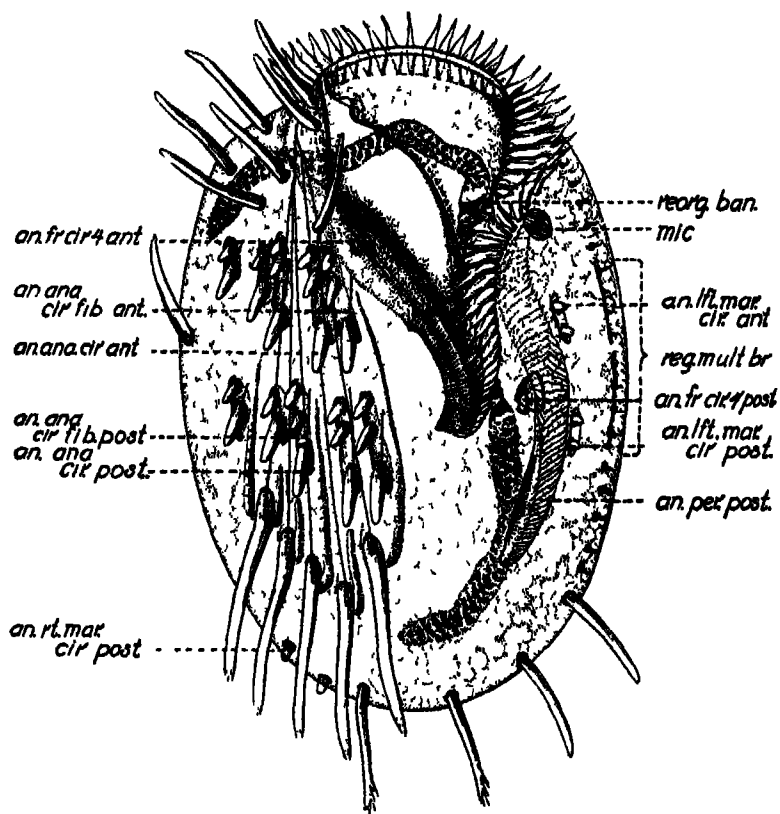
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PLATE 1



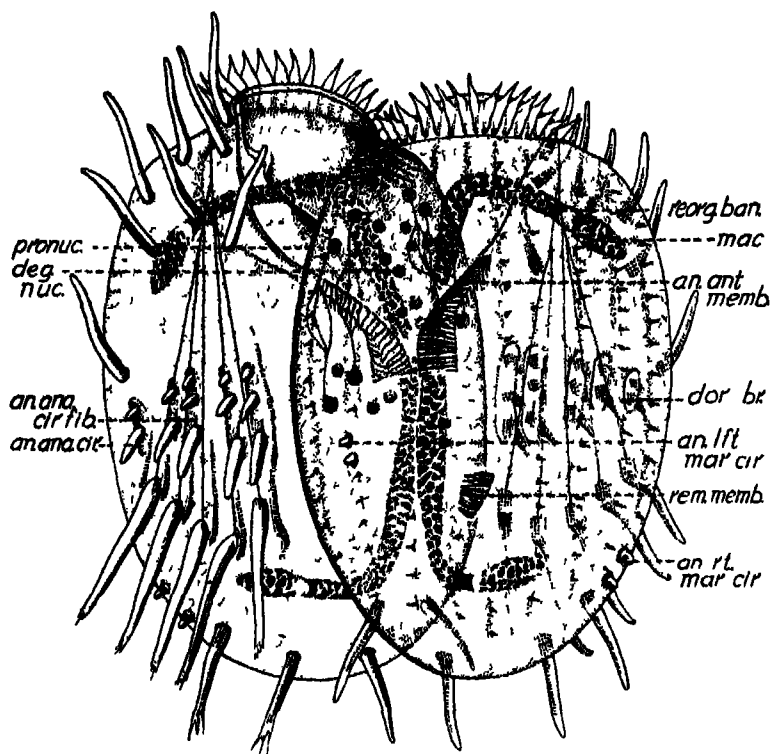
Euplates patella, ventral view, from living organisms X 600. *abr ana cir*, anal cirrus, *ana cir fib*, fibril of anal cirrus, *con vac*, contractile vacuole, *cytophar*, cytopharynx; *cyt rec*, cytostomal recess, *fr cir*, frontal cirrus, *mac*, macronucleus, *mar. cir*, marginal cirrus, *memb*, membranelles, *vent br*, ventral bristles, *vent cir*, ventral cirrus.

PLATE II



Ventral view of stage in binary fission, showing the new sets of cirri and fibrils, the new peristome, and the multiplication of the bristles. Schaudinn's, alcoholic haematoxylin $\times 600$. *an.ana.cir.ant.*, anlage of anal cirrus for anterior daughter, *an.ana.cir.post.*, anlage of anal cirrus for posterior daughter, *an.ana.cir.fib.ant.*, anlage of fibril of anal cirrus for anterior daughter, *an.ana.cir.fib.post.*, anlage of fibril of anal cirrus for posterior daughter, *an.fr.cir.4.ant.*, anlage of frontal cirrus 4 for anterior daughter, *an.fr.cir.4.post.*, anlage of frontal cirrus 4 for posterior daughter, *an.lft.mar.cir.ant.*, anlage of left marginal cirrus for anterior daughter, *an.lft.mar.cir.post.*, anlage of left marginal cirrus for posterior daughter, *an.per.post.*, anlage of peristome for posterior daughter, *an.rl.mar.cir.post.*, anlage of right marginal cirrus for posterior daughter, *mic*, micronucleus, undergoing mitosis, *reg.mult.br*, region of multiplication of bristles, *reorg.ban.*, reorganization band of macronucleus.

PLATE III



Stage in conjugation illustrating reorganization of the gamete. Organism at right in dorsal view. Organism at left in ventral view. The posterior portion of the peristome has been resorbed, and a new anterior portion is being differentiated, as well as new sets of cirri. Pronuclei in process of formation. Schaudinn's, alcoholic haematoxylin $\times 600$. *abr*, an *ana. cir.*, anlage of anal cirrus, *an. ana. cir. fib.*, anlage of fibril of anal cirrus, *an. ant. memb.*, anlage of anterior portion of membranelle zone, *an. left. marg. cir.*, anlage of left marginal cirrus, *an. right. marg. cir.*, anlage of right marginal cirrus; *deg. nuc.*, degenerating nuclei, *dors. br.*, dorsal bristles, *mac*, macronucleus; *pronuc.*, pronucleus, *rem. memb.*, remnant of posterior portion of membranelle zone in process of resorption, *reorg. ban.*, reorganization band of macronucleus.

OBITUARY

HOWARD McCLENAHAN

HOWARD McCLENAHAN was the son of John Megredy McClenahan and his wife Laura Jane (Farrow) McClenahan. He was born on October 19, 1872, at Port Deposit, Maryland, where his family operated extensive granite quarries. He entered Princeton University in the class of 1894, and by specializing in his Senior year and taking an extra year, he was graduated in 1895 with the advanced degree of Electrical Engineer. After two years spent in the practice of his profession he returned to Princeton as Instructor in Physics. He proved to be an excellent and inspiring teacher, and after passing through the grade of Assistant Professor was appointed Professor of Physics and Electrical Engineering in 1906. His technical knowledge was of great service in the designing and equipment of the Palmer Physical Laboratory. In 1912 he was appointed to the office of Dean of the College, in which he was in charge of the discipline of the students. He remained in this office until his resignation in 1925. He was warmly interested in the young men under his charge, and was sympathetic with their points of view, so that he was able to administer his office with sufficient firmness and yet without losing the students' confidence and regard. When he resigned in 1925 the Senior Class made him an honorary member of the class, and at a dinner held in his honor, presented him with a very handsome watch as a token of their affection. He was for many years Chairman of the Board in charge of the athletic interests of the University, and in this position did all that he could to maintain the standards of eligibility set for those who represented the University in athletic contests, and to inculcate the right attitude of the student body to athletic sports. The temporary criticism which he inevitably encountered for some of

his decisions never resulted in a permanent loss of confidence in his wisdom or impartiality.

Soon after the Great War broke out, McClenahan was sent abroad by a group of Princeton Alumni, to investigate the conditions in Belgium and among the Belgian refugees in England, with the view of recommending the methods by which assistance could most usefully be given.

In 1925 McClenahan accepted the post of Secretary of the Franklin Institute in Philadelphia. He took up his work in the old building on Seventh Street, which was in many ways inadequate for the hoped for development of the Institute, and yet was fitted by long use and by tradition to serve in that development. He appreciated from the start the value of ceremonial in calling attention to the importance of the Institute. In his first year he instituted Medal Day, on which the medals bestowed each year on certain distinguished inventors and scientific men were presented to their recipients in a formal gathering. These Medal Days have attracted from year to year an increasing attendance of distinguished scientific men, and have become important in the scientific life of the country. He set himself also to improve the *Journal* of the Institute by obtaining for it articles of increased interest and wider appeal. Having in mind Faraday's Christmas lectures "adapted to a juvenile auditory," he fostered the James Mapes Dodge Lecture Foundation for Young People, which from year to year provides a center of attraction for young people who have an interest in science. He also guided the development of the Bartol Research Laboratory, and its final establishment at Swarthmore.

Many influential citizens of Philadelphia had for some time wished to establish a memorial to Benjamin Franklin, who had contributed so much to the development of that city. McClenahan felt that no memorial could be more suitable than an industrial and technical museum. After careful study of some of the great museums in Europe he presented a plan to the Board of Directors of the Institute, who received it with enthusiasm. With the cooperation of

several wealthy men, of various civic bodies and of the City Councils, a great building was speedily erected on the Parkway and adequately equipped with exhibits. McClenahan was made Director of the Museum, and he served in that post in addition to serving as Secretary of the Institute, until his failing health made necessary some lessening of his duties. The value of his work was recognized by honorary degrees from several important institutions of learning, and also by his appointment as an honorary member of the Royal Institution of Great Britain and as a Director of the Deutsches Museum in Munich. He served as a Trustee of Lincoln University and as an Associate Trustee for Graduate Study of the University of Pennsylvania. He was elected to the American Philosophical Society in 1931.

McClenahan was a man of genial and winning manners, and won the regard and affection of those who worked with him and under him. He was able to plan on a large scale, and was equally able to attend to and decide upon the many details of a complex organization. The enormous amount of work undertaken by him in connection with the development and equipment of the Benjamin Franklin Memorial proved too much for his strength and he felt compelled in 1935 to resign his post as Director of the Museum, and to take a year's leave of absence from his post as Secretary of the Institute. While on this vacation, which it was hoped would enable him to recover his energy and resume his work, he died suddenly from heart failure at Winter Park, Florida, on December 17, 1935.

WILLIAM F. MAGIE

INTEGUMENTARY COLOR CHANGES OF ELASMOBRANCH FISHES ESPECIALLY OF *MUSTELUS*

G. H. PARKER

(Read November 27, 1936)

ABSTRACT

Squalus acanthias is a dark dogfish that shows little or no evidence of a pale phase. As it blanches somewhat on loss of its pituitary gland its general darkness indicates a certain continuity of pituitary secretion independent of its environment. *Mustelus canis* and *Raja erinacea* show well marked dark and pale phases in response to changes in their surroundings.

The dark phase in these three elasmobranchs is due to a neurohumor from the intermediate lobe of the pituitary gland carried in the blood from the gland to the melanophores, a hydrohumor. This substance, contained in commercial pituitrin and in intermedin, is different from the oxytocic and the pressor principles from the pituitary gland.

The pale phase in these fishes is due to the absence from the blood of any dispersing factor (*Raja erinacea*), or to the action of nerves (*Mustelus canis* and *Squalus acanthias* in part). In these three elasmobranchs there is no evidence of a W-substance such as has been found in *Scyllium* and in some species of *Raja* by Hogben.

The pinkness of pale elasmobranchs may be as much due to the exposure of the dermal blood-vessel by pigment concentration as to the absence of a pressor factor. The color changes in elasmobranchs are slow in accomplishment involving hours and days, a condition associated with their usual means of excitation, chiefly hydrohumors.

Adrenalin blanches *Mustelus canis*, *Squalus acanthias*, and *Raja erinacea* but probably plays no part in the natural paling of these fishes. The concentrating neurohumor in such elasmobranchs as *Mustelus* and *Squalus* is not carried by the blood, it is a lipohumor. It is soluble in olive oil, ether, but not in water. It resists heat to 110° C., the action of sodium hydroxide and of hydrochloric acid. It is a relatively stable compound, possibly a sterol.

I INTRODUCTION

In teleost fishes the integumentary color changes have been matters of interest since the earliest times, but in elasmobranchs these changes have received attention only during the last decade and a half. Brief as this period is it has been long enough to show that the color changes in cartilaginous fishes are in many respects like those in other animals particularly in that they are brought about in different species by means often strikingly diverse and even unique. According to various investigators animals with active

Contribution No. 131 of the Woods Hole Oceanographic Institution

chromatophores, particularly melanophores, may become normally dark in several ways: through the direct action of light on the skins of enucleated forms including fishes (Pouchet, 1871), through the action of the neurohumor carried in the blood from the intermediate lobe of the pituitary gland, as in almost all chromatic vertebrates (Hogben, 1924); through the lipohumors from the dispersing nerve-fibers of certain fishes, such as *Fundulus* and *Ameiurus* (Parker, 1933a, 1934b), and probably through other means still to be discovered. They may become pale in some half a dozen different ways: through the direct effect of darkness upon the skin of blinded animals as salamander larvæ (Babák, 1910) and fishes (von Frisch, 1911), through the action of adrenalin transported by the blood, as in *Phrynosoma* (Redfield, 1918); through the mere absence from the animal's blood of a dispersing agent such as the pituitary neurohumor as was originally claimed for amphibians (Hogben and Winton, 1922), through the neurohumor from the *pars tuberalis* of the pituitary complex, as in certain toads and frogs (Hogben and Slome, 1931), and through the lipohumors from the concentrating nerve-fibers of *Fundulus* and other fishes (Parker, 1934a). When one keeps in mind that this catalogue of the means of melanophore change is assuredly incomplete and that any given species may employ not only one or other of these means but combinations of them, the room for diversity in the mechanisms controlling color responses must be admitted to be considerable. As the following discussion will show, more or less of this diversity is realized in even so compact a group of vertebrates as the elasmobranchs where, so far as our present information goes, scarcely any two species employ identical means for color change.

The fishes upon which the following studies were based are the smooth dogfish, *Mustelus canis*, the spiny dogfish, *Squalus acanthias*, and the skate, *Raja erinacea*, all from the region about Woods Hole. The work was done in part at the Oceanographic Institution and in part at the Marine Biological Laboratory both at Woods Hole. To the Directors

of these two institutions and to their very efficient corps of assistants I wish to extend my sincere thanks. The special expenses of the research were met by a generous grant from the Milton Fund of Harvard University to whose administrative officers I am under great obligation.

2. TECHNIQUE

The only special feature in the technique of the problem that calls for comment was the use of cold as a stupefying agent in place of drugs. The profound and somewhat lasting effect of the common anesthetics such as ether, urethane and the like on chromatophores led me to stupefy by means of cold. It was found very convenient to immerse fishes in a mixture of cracked ice and seawater for stupefaction. After a quarter of an hour or so in such a mixture the fish was found to have become fully passive and on removal from the cold it remained in this condition for ten to fifteen minutes during which an operation could be easily carried out. All the operations were of a relatively simple character and were usually completed in at most ten minutes. After the operation the fish was placed in an aquarium of seawater where it recovered quickly, for there was no drug to be eliminated. The advantage of this method of stupefaction over those in which drugs are used is obvious. The ice mixture was put in any small vessel for small fishes and in a barrel or tub for large ones. This method ought to find easy application for the stupefaction of any cold-blooded animal.

3. NORMAL COLOR RESPONSES

A number of elasmobranchs appear to be almost if not quite devoid of color responses to such surrounding changes as would call forth active alterations of tint in many other fishes. *Raja clavata* and *R. batis*, both described as darkish species, are said by Schaefer (1921) not to change in color at all on being transferred from a black to a white background. *Squalus acanthias*, a dark dogfish, when introduced into an illuminated aquarium with white walls, will ordinarily show

no change of tint though some individuals under such circumstances will in the course of two days blanch slightly. These moderately pale fishes on being transferred to a tank with black walls will slowly reassume their original dark color. After the complete removal of the pituitary gland from any dark *Squalus* the fish will blanch slowly even in a tank with black walls (Parker, 1936a). This observation has been confirmed by Hogben (1936) on *Raja clavata* which though a normally dark inactive species, as originally noted by Schaefer, will also blanch on the loss of its pituitary gland. Both *Scyllium catulus* and *S. canicula* appear to be relatively inactive in their color changes (Young, 1933, Hogben, 1936; Wykes, 1936). Like *Squalus acanthias* and *Raja clavata* they also blanch somewhat on the loss of their pituitary glands. Notwithstanding the fact that all these relatively inactive, dark forms show very little or no color response to changes in their environment, their dark color can not be attributed to a complete lack of ability to change their tint, for on the loss of their pituitary glands they blanch noticeably. Their more or less constant dark coloration is therefore probably due to a steady production of a dispersing pituitary neuro-humor, a production which is apparently not influenced to any considerable extent by environmental changes.

In contrast with these inactive elasmobranchs may be placed a number of active species of which the color responses to environmental differences are pronounced and unquestionable. *Mustelus canis*, of which extreme differences in tint were first noted by Lundstrom and Bard (1932) in their experiments on the pituitary gland in this fish, is dark on a black background and very pale on a white one (Parker and Porter, 1934). Adult fishes change from the pale to the dark phase in from half an hour to two hours. The reverse change from dark to pale requires some two days. The two phases in *Mustelus* are so strikingly associated with the environmental conditions that it is strange that Hogben (1936) could have had any doubt on this matter. The pups of *Mustelus canis* immediately after birth are fully responsive in their color

changes to the condition of their surroundings (Parker, 1936b). These young fishes change from pale to dark in less time than from dark to pale as is characteristic of the adults. Other elasmobranchs that show active color responses are *Raja erinacea* (Parker, 1933b), *R. brachyura*, *R. maculata*, and *Rhina squatina* (Hogben, 1936; Wykes, 1936). In all these forms the color changes are recorded as from the dorsal aspect of the fishes. In *Raja oxyrhyncha* Weidenreich (1927) has described a change of tint that takes place on the ventral surface of this species, a remarkable and somewhat puzzling phenomenon.

4 THE DARK PHASE

The dark phase of elasmobranchs so far as it has been studied appears to be excited exclusively by pituitary secretions. This was first made clear by Lundstrom and Bard (1932) in their study of *Mustelus*. When the pituitary gland is removed from this and other elasmobranchs the fishes invariably become pale, some more, others less (*Mustelus canis*, Lundstrom and Bard, 1932, *Squalus acanthias*, Parker, 1936a, *Scyllium canicula*, *S. catulus*, *Rhina squatina*, *Raja brachyura*, *R. clavata*, *R. maculata*, *R. microcelatus*, Hogben, 1936, Wykes, 1936, Waring, 1936a, 1936b). An injection of an extract from the pituitary gland into such pale elasmobranchs is always followed by a darkening of their integument. No other organ than this gland is known to be connected thus with the dark phase of these fishes. If the blood of a dark *Squalus* is injected into a slightly pale one, a dark spot is produced though such blood has no effect on a dark fish. Blood from a pale fish is without influence on either dark or pale individuals (Parker, 1936a). What is true of the blood of *Squalus* appears also to be true of that of *Mustelus* (Parker and Porter, 1934). These observations have convinced most investigators that the dark phase of elasmobranchs is excited by a neurohumor produced in the pituitary gland and carried thence by the blood to the responding melanophores.

It is generally assumed that the production of this neurohumor is controlled through the eyes of the fish and to a

considerable extent this is true. When the eyes of *Mustelus* are removed the fish will within a few hours assume a dark tint which is then maintained with more or less constancy irrespective of the surroundings. In some instances the coloration may be extreme in depth (Parker and Porter, 1934). In *Raja brachyura*, according to Hogben (1936), the eyeless fish takes on a tint between pale and dark. If from a blinded dark *Mustelus* the pituitary gland is removed, the fish soon becomes fully pale, showing that the dark phase of the blinded individual was still dependent upon the pituitary neurohumor. The exclusion of the eye from any direct control over this tint in the fish is seen from the fact that a hypophysectomized and consequently pale fish does not change its tone to any observable degree on being enucleated. The eyes are concerned with the control of the gland only from the standpoint of environmental changes exciting or inhibiting it in response to the state of the surroundings. A smooth dogfish whose optic nerves have been cut darkens in precisely the same way as one whose eyes have been removed. Such a condition shows that the control exerted by the eyes of this fish over its pituitary gland is not through a hormone given out by the retina or other such part, and carried by the blood to the pituitary gland, but by nerve impulses transmitted from the retina over the optic nerve to deeper parts.

The neurohumor produced by the pituitary gland and concerned with the dispersing of pigment in the elasmobranch melanophores has been shown to come from the posterior or neuro-intermediate lobe of the gland (*Mustelus*, Lundstrom and Bard, 1932, *Raja brachyura*, *R. maculata*, Hogben, 1936, *Scyllium canicula*, Waring, 1936a). Extracts from this part of the gland always act as darkening agents. The commercial pituitary products "puitritin" (Parke, Davis and Co.) and "infundin" (Burroughs, Wellcome and Co) both darken *Mustelus* (Lundstrom and Bard, 1932, Parker, 1935b) and the former has been shown to darken *Squalus* (Parker, 1936a). Through the kindness of Dr. F. L. Hisaw I was enabled to test samples of intermedin made in his laboratory by Dr. H.

L. Fevold.¹ Intermedin is a pituitary extract which by its method of production is freed from the oxytocic and vaso-pressor principles contained in ordinary pituitary extract. It is convenient to express the concentration of intermedin, as described in the accompanying note, on the basis of the amount of extract derived from one gram of dry gland and dissolved in one cubic centimeter of water. In the actual tests 0.5 cc of solution at various dilutions was injected hypodermically into the sides of pups of smooth dogfishes. Each pup weighed about 100 g. and had a length of some 35 cm. The results of these injections are shown in table I.

TABLE I

Color responses of three sets of smooth dogfish pups (*Mustelus canis*) I, II, and III, into each of which 0.5 cc of an aqueous solution of intermedin had been injected. The full strength solution of intermedin is assumed as that in which the extract from 1 g of dry pituitary gland is contained in 1 cc. of water. The dilutions are expressed in the fractions of grams of dry gland substance that yielded the extract injected. The dogfishes in the beginning were pale and were kept in an illuminated aquarium with white walls.

Grams of Dry Gland as Source of Extract in 0.5 cc. Water	Integumentary Tints of the Three Sets of Dogfishes		
	I	II	III
0.2	Dark	Dark	Dark
0.1	Dark	Dark	Dark
0.05	Darkish	Darkish	Dark
0.025	Pale	Darkish	Pale
0.0125	Pale	Pale	Pale
0.00625	Pale	Pale	Pale
H ₂ O	Pale	Pale	Pale

As table I shows 0.5 cc. of intermedin solution may darken a smooth dogfish pup when the concentration of the solution

¹The intermedin used in these experiments was prepared by Dr. H. L. Fevold from powdered, whole, pituitary glands of sheep. The solution of intermedin was an 80 per cent ethanol soluble fraction of an alkaline extract of the powdered gland. The ethanol was evaporated and the residue was dissolved in water so that each cubic centimeter of water contained the extract from 50 grams of the original pituitary powder. This was used as a stock solution and various dilutions as desired were made from it. Amounts of intermedin injected into dogfishes could therefore be expressed as equivalent to a given number of grams of the original powder. Thus a 0.2 gram solution was one in which each cubic centimeter of fluid contained an amount of extract that was obtained from 0.2 gram of the dry, powdered gland.

is such as is obtained from 0.025 g. of dry gland in 0.5 cc. of water. Weaker than this the solution is ineffective; stronger it is invariably effective. The dispersing neurohumor for elasmobranch melanophores must be contained in such extracts though it cannot be stated in how pure a form it exists. This neurohumor, the B substance of Hogben, must also be contained in commercial infundin and pituitrin but not in pitocin (Parke, Davis and Co.) which, though it is the carrier of the oxytocic principle, does not darken dogfishes (Lundstrom and Bard, 1932). I agree with Hogben (1936) in the belief that this neurohumor is not the same as the pressor substance contained in pitressin, for, though pitressin was found by Lundstrom and Bard to darken dogfishes, it did so, I suspect, not because of the pressor substance it contained but in consequence of a certain amount of true dispersing neurohumor included in the pitressin as an accidental impurity.

Excepting by means of the dispersing neurohumor of the intermediate lobe of the pituitary gland I know of no way of profoundly darkening the elasmobranch skin. This blood-soluble neurohumor appears to be the one and only agent thus directly concerned with the dark phase. In eyeless selachians, and in probably many other blinded animals, it seems to be continuously produced and the animals remain in consequence moderately dark. When the eyes are functional and the fishes are on an illuminated black background it is present in large amount, on a white background it may be entirely absent probably as a result of glandular inhibition excited through the eyes by the white surroundings. It must not be forgotten that eyeless *Mustelus* from which the pituitary gland has been removed are often still able to show a slight color change, darkening in bright light and blanching in darkness, reactions which are probably due to the direct effect of the light or its absence on the melanophores.

5 THE PALE PHASE

The blanching of elasmobranchs is a more intricate process than their darkening. It may be due to the mere absence of an agent active in dispersing pigment, as was implied by Lundstrom and Bard (1932). It may result from the action of concentrating nerves, as was advocated by Parker and Porter (1934). It may be occasioned by the presence of an active concentrating neurohumor, as has been maintained recently by Hogben (1936). Or it may be the outcome of factors still to be discovered. Among the various means that have been proposed thus far as the exciting agents in the blanching of these fishes no instance of mutually exclusive elements has occurred; hence in any given elasmobranch these suspected agents may be present singly or in any combination. In discussing the means by which elasmobranchs may blanch I shall begin with a consideration of a concentrating pituitary hormone.

Hogben's contention that elasmobranchs blanch as a result of a concentrating hormone called by him the W substance, which excites the pale phase in these fishes as the dispersing pituitary hormone excites the dark one is set forth in his most recent paper on this subject (1936). This view is an extension to elasmobranchs of conclusions originally arrived at by Hogben and Slome (1931) from their study of amphibians. The evidence advanced by Hogben in favor of this view as applied to sharks and rays is drawn from a study of *Scyllium canicula*, *S. catulus*, and *Raja brachyura*. Hogben believes that the W substance in these fishes is derived from the anterior pituitary lobe. When in a dark fish this lobe is removed no change in color is noted. If this lobe is removed from a pale fish, however, the creature becomes dark even though it is kept on a white background, an observation confirmed by Waring (1936a). Thus the loss of the anterior lobe abolishes temporarily and perhaps permanently the pale response. Implanting an anterior lobe into a pale fish produced negative or relatively slight results. Implanting such a lobe into a dark fish produced so slight a change as to

justify no definite conclusion. As Hogben remarks the inconclusiveness of much of this work is due in large measure to the difficulties in managing marine animals, a hindrance that is familiar to every one who has worked on selachians. From results almost identical with these Waring (1936a) was led to conclude that in *Scyllium* the anterior pituitary lobe, though not directly concerned with blanching, was the means of activating the immediate mechanism for this operation, a mechanism which according to this worker may be either humoral or nervous but which at present is quite obscure.

When the anterior pituitary lobe of *Mustelus* is removed, the fish will continue to change from pale to dark and the reverse in an entirely normal way. This dogfish, however, possesses concentrating nerve-fibers and hence these fibers may replace the possible activity of the anterior pituitary lobe. However the removal of the whole pituitary complex, as has long been known, will induce the fish to assume in a short time a maximum pallor even in a black-walled illuminated reservoir. This observation, first made by Lundstrom and Bard, has been repeated often by others and shows conclusively that the pituitary gland, including its anterior lobe, is not necessary for the complete blanching of this fish. It does not, however, allow the conclusion to be drawn that this gland may not play some part in this process. What is true of *Mustelus* is for the most part true of *Squalus* where concentrating nerve-fibers are few or in certain individuals probably entirely absent. A more conclusive instance, however, is seen in *Raja erinacea* where nerves have no part whatever in blanching. In this species the loss of the pituitary gland is followed by a maximum paling showing clearly that this operation may be fully completed in the absence of this gland.

If a concentrating pituitary neurohumor, such as the W substance of Hogben is believed to be, is present in selachians, it ought to be identifiable in the blood of these fishes when they are in the pale state. Tests to this end were carried out on the three common species at Woods Hole and have been

reported already in part. Such tests consisted in the transfer of a certain amount of blood from pale fishes to moderately dark ones on the assumption that the partly dispersed pigment in the melanophores of the recipients would thereby be concentrated. Of the score or more tests of this kind that have been carried out on *Mustelus canis* (Parker and Porter, 1934) and on *Squalus acanthias* (Parker, 1936a) none has ever given a positive result. In all instances the dogfishes into which the injections were made neither developed pale spots nor changed noticeably in tint.

Another set of tests which were directed particularly at this question were carried out in *Raja erinacea*. This skate has been shown quite clearly to have no nervous control over its melanophores. It nevertheless changes from pale to dark and the reverse in a very clear and unmistakable manner (Parker, 1933b). At three different times when this species was sufficiently abundant at Woods Hole tests were made in the following way. Two medium-sized skates were kept some two to three days in an illuminated tank with black walls till the fishes were fairly dark. At the same time a third skate was kept in an illuminated white-walled tank till it was completely pale. This pale fish was then fully bled from the caudal artery, the blood thus obtained was defibrinated, and 1 cc. of it was injected into a pectoral fin of one of the two dark skates, the other being held for comparison. Both dark skates, now together in the same black-walled, illuminated aquarium, were kept under close inspection over a period of some eight hours. At no time during this interval was the injected skate seen to develop a pale spot in the region of the injection nor to change its general tint. The other two tests, which were essentially like the one just described, also yielded no evidence in favor of a blanching hormone in the blood of the pale fish. The same technique when applied in a reciprocal way to the blood of a dark individual regularly yielded satisfactory evidence of a dispersing neurohumor, a result that indicates the reliability of the procedure. I therefore conclude that at least in *Raja*

erinacea the pale phase is not due to a concentrating pituitary neurohumor carried in the blood such as the W substance hypothesized by Hogben. Whether this conclusion will hold for other elasmobranchs than *Raja erinacea* and particularly for those forms from which both Hogben and Waring removed the anterior pituitary lobe and thus abolished blanching remains to be determined. Different species of fishes show in the details of their color control great diversity.

A second suggested way by which elasmobranchs may blanch is through the absence in their blood of any dispersing neurohumor. This implies that a melanophore when left to itself naturally drifts into a state with concentrated pigment, an assumption often met with but by no means established. This general explanation of blanching was adopted by Hogben (1924) in his early work on amphibians but was eventually discarded by him. As already noted it is implied but not precisely expressed by Lundstrom and Bard (1932) in their study of *Mustelus*. In this dogfish, as the work of Parker and Porter (1934) shows, the pale phase involves concentrating nerves and consequently it is difficult to say whether this second method of blanching can be said to apply or not to *Mustelus*. With *Raja erinacea* the case is quite different. This fish, as already pointed out, darkens in consequence of a dispersing pituitary neurohumor in its blood. It blanches in a clear and obvious way and yet it appears to have no concentrating nerves and its blood when transferred gives no evidence of containing a concentrating neurohumor. There seems to be little left to fall back upon as an explanation of how this fish assumes its pale phase except the supposition that the gradual disappearance of the dispersing substance from its blood allows its melanophores of themselves to concentrate their pigment. This assumption is not without a certain amount of support, for the same condition has appeared in certain American frogs recently studied in the Harvard Laboratories, a condition unlike that reported a short time ago by Hogben for South African and European amphibians. Whether or not this explanation of blanching holds for the

selachians studied by Wykes (1936) cannot be stated. In *Raja brachyura*, *R. maculata*, *Rhina squatina*, *Scyllium canicula* and *S. catulus*, there is good evidence according to this investigator for the conclusion that nerves play no part in color changes, but whether these fishes blanch in consequence of the presence of a concentrating neurohumor or of the absence of a dispersing one cannot be affirmed till such tests as, for instance, those involving transfers of blood have been tried.

Although the evidence here brought forward so far as the present problem is concerned must be admitted to be fragmentary and inconclusive for *Mustelus* and *Squalus* that for *Raja erinacea* is quite otherwise. The pale phase of this ray is due neither to direct nervous action nor to a concentrating neurohumor in its blood. It appears to result from the mere absence of a dispersing factor.

The third view as to the blanching of elasmobranchs is that this operation depends upon the direct action of concentrating nerves on the melanophores in these fishes. The evidence for this conclusion has already been presented in a series of papers (Parker and Porter, 1934, Parker, 1935a, 1935b, 1936a, 1936b, 1936c) dealing with *Mustelus*. When a cut is made into the substance of a moderately dark *Mustelus canis*, especially through a fin of this fish, so as to sever integumentary nerves there appears in the course of ten to fifteen minutes a pale splotch or band which extends from the region of the cut over the skin, for instance, to the edge of the fin. These light areas follow the distribution of the nerves, not that of the blood-vessels (Parker and Porter, 1934). They can be excited by electric stimulation as well as by cutting (Parker, 1935a). After they have faded they can be revived by a new cut (Parker, 1936c). They result from a concentration of pigment in the melanophores and the evidence thus far accumulated points conclusively to them as the result of the temporary activation of concentrating nerves. They are noticeable in pale dogfishes as well as in dark ones showing that their method of excitation is on

the whole more efficient than that by which the normal paling of this fish is elicited. They are as easily excited in the pups of *Mustelus* as in the adults (Parker, 1936b). Thus there appears to be perfectly good ground for the belief in the presence of concentrating nerve fibers in this dogfish and that these fibers are concerned with its pale phase.

That all elasmobranchs are not thus provided with fibers of this class seems also equally certain. As early as 1933 Young in his exhaustive paper on the autonomic nervous system of selachians pointed out that in *Scyllium* no change in color was observed after section of the spinal, trigeminal, or facial nerves. He was therefore led to conclude that there was no direct nervous control of the melanophores in this fish. These observations were in support of his findings that in the deep-seated autonomic connections in this and other selachians there were no gray rami communicantes, tracts over which the postganglionic nerve-fibers controlling color changes pass from the sympathetic ganglia to the spinal nerves and thence to the melanophores. So far as the absence of color changes due to the cutting of nerves is concerned Young's observations on *Scyllium* have been confirmed by Waring (1936a) as well as by Wykes (1936) who also has shown that nerve section in *Raja brachyura* and *R. maculata*, and nerve stimulation in *Raja brachyura*, *Rhina squatina* and *Scyllium catulus* fail to induce color changes. As already noted the section of pectoral nerves in the American *Raja erinacea* (Parker, 1936) is without effect on the color of this species. In *Squalus acanthias* on the other hand individuals differ, in some instances faint bands result from the section of nerves, in others not. Thus this species seems to hold a somewhat intermediate position between *Mustelus*, the blanching of which is nervous and a considerable number of other selachians, *Scyllium*, *Raja*, and *Rhina*, in which it is non-nervous. Whether in these three forms blanching is due to a pituitary neurohumor such as the W substance of Hogben or to the mere absence from the blood of a dispersing neurohumor cannot be stated with certainty though from what

has been presented concerning *Raja erinacea* it seems probable that the hypothesis of absence is the correct one

6 ADRENALIN

Adrenalin almost invariably induces pigment concentration in the vertebrate melanophores. It is therefore natural to suspect this hormone in any instances where concentration of pigment occurs and where other exciting agents have not been identified. Lundstrom and Bard (1932) were the first to point out that adrenalin blanched elasmobranchs. When 1 cc. of a 1 : 1000 solution of adrenalin hydrochloride was injected into a smooth dogfish the fish, according to these authors, began to pale in some ten minutes. This blanching reached a maximum in about an hour and persisted approximately two hours. The dose of adrenalin was admittedly enormous. This result was confirmed by Parker and Porter (1934) who found that 0.5 cc. of 1 : 10,000 would induce a temporary blanching in an adult smooth dogfish. *Mustelus* pups reacted to this hormone in much the same way as adults did (Parker, 1936b). Young (1933) was unable to induce pallor in *Scyllium canicula*, *S. catulus* and *Torpedo ocellata* by the injection of 1 mg. of adrenalin hydrochloride, though this dose was amply sufficient to blanch *Pleuronectes*. Wykes (1936) was able to produce only a small degree of pallor in *Raja brachyura* and *Rhina squatina* by injecting 1 cc. of a 1 : 10,000 adrenalin hydrochloride, a change which she is inclined to attribute to vaso-constrictor action. Possibly in Young's tests and certainly in those by Wykes the concentrations used were very close to the effective limits of this hormone judged from the data given for *Mustelus*. Here the effective doses were truly prodigious. In fact they were so large that it is incredible that this hormone, even though it does cause concentration of pigment in a number of elasmobranchs, can be a normal physiological agent in inducing such changes. That the blood of pale elasmobranchs, *Mustelus*, *Squalus*, and *Raja*, has no effect whatever on the melanophores of dark or partly dark individuals leads to the

conclusion that in those selachians tested adrenalin probably plays no part in their blanching (Waring, 1936a).

7. PINKNESS OF THE PALE PHASE

Almost all who have worked extensively on the color changes of elasmobranchs have been struck by the pinkness which often accompanies the pale phase. This was noticed in *Mustelus* by Lundstrom and Bard (1932) and by Parker and Porter (1934). It is also recorded by Hogben (1936) for certain skates from which he had removed the pituitary glands. Hogben following a suggestion by Krogh (1922) was inclined to attribute this pinkness to the absence of the pressor principle from the blood of the hypophysectomized fishes. Although this explanation may apply to a certain degree it must not be forgotten that elasmobranchs which have blanched normally also take on a pink hue. Thus if a *Mustelus* is put in a white-walled illuminated tank, it will become pale in the course of about two days toward the end of which period the pink tone gradually asserts itself. It is of course possible that during this time pressor substance may have gradually diminished in the blood and the blood-vessels in consequence may have become enlarged, but it is also true that by the concentration of melanophore pigment the integumentary vessels become more readily visible. Certainly the pink tint which is acquired as dogfishes blanch normally is due in part if not in whole to the mere exposure of the blood vessels irrespective of their change in calibre.

8 THE CONCENTRATING NEUROHUMOR

The pale phase of *Mustelus* has already been shown to be due to the direct action of concentrating nerves on the melanophores of this fish (Parker and Porter, 1934). These nerves have been suspected of acting on the color cells through an oil-soluble substance discharged from their terminals, a suspicion that has been justified by the extraction of such a substance from the fins of pale *Mustelus* (Parker, 1935b). Olive oil extracts, cold ether and Soxhlet ether extracts of

pale fins of *Mustelus* when injected subcutaneously into a dark individual induce the concentration of its melanophore pigment. Injections of seawater, of pure olive oil, of olive-oil extracts of dark fins or of muscle, seawater extracts of pale fins, and defibrinated blood from pale or from dark fishes have no effect whatever on the integumentary color of this dogfish. In consequence of these observations the concentrating agent in *Mustelus* is believed to be an oil-soluble hormone, a lipohumor, of nervous origin.

To carry this inquiry toward a more quantitative stage efforts were made to standardize the effective extract. The fins of three adult smooth dogfishes that had been well blanched in the course of several days were cut off and dried over night in a chemical oven held at a temperature between 105° and 110° C. The weight of the dried fins was 72.4 g. These dry fins were then thoroughly pulverized and extracted in a Soxhlet apparatus with ether over a period of six hours. The Soxhlet waterbath had a temperature of about 65° C. and a turnover of once in about 20 minutes. The ether extract thus obtained was yellowish in color and after full evaporation left a thick, yellowish, oily residue which from the three sets of fins weighed 1.02 g. This residue was mixed with an equal volume of cold-blooded Ringer's solution and the mixture thus obtained was regarded as standard. From this standard mixture dilutions were made by adding appropriate amounts of pure Ringer's solution. Dilute mixtures prepared in this way were then tested by being injected hypodermically into the dorsal flank of a *Mustelus* pup (approximate length 35 cm, and weight 100 g.). The amount introduced into the pup was 0.05 cc. and the fish was subsequently watched for any color change. The results were comparatively simple. The standard mixture and that composed of one part of standard and one part of Ringer's solutions invariably produced pale spots on the skin of the fishes. Dilutions of one part of the standard mixture in ten, fifty, one-hundred, and one-thousand parts of Ringer's solution induced no color change at all. Plainly the standard mixture,

so-called, is not far from the limit of physiological efficiency. This result led me to repeat a test which I had previously carried out and which had yielded rather contradictory results. In table I of my former paper (Parker, 1935b) I entered the observation that an olive-oil extract from the pale skin of *Mustelus* had failed in the two dark fishes tested to induce local blanching. This observation was clearly opposed to the records in the upper part of the table where it was shown that oil extracts from pale fins had commonly given such reactions. If a pale fin yields an extract that will blanch a spot on a dark fish why will not a whole skin from a pale fish do the same? It occurred to me after I had made the standardization determinations that the probable answer to this question had to do with the concentration of the extracts. Possibly the oil extract from the skin was more dilute than that from the fins and hence the failure of the former extract to produce a pale spot. I therefore repeated this test and instead of extracting one pale dogfish skin with olive oil, as I had formerly done, I extracted three such with ether in a Soxhlet apparatus. These together yielded a residue of 0.8 g. of oily material. On mixing this residue with an equal volume of Ringer's solution and injecting 0.05 cc. of it into three dark pups pale patches appeared in every instance. I am therefore convinced that my first tests with skin extracts were made with too dilute a mixture and that when a strong skin extract is made it is as effective for blanching as the extracts from the fins. If the fin which shows a striking color change yields an effective extract, the skin of the flanks and dorsum which also changes color ought likewise to yield a similar product and apparently it does.

While these extractive operations were in progress other parts of the dogfish's body not previously tested were tried out. Soxhlet ether extracts of the brain and spinal cord were made and yielded relatively large amounts of residue which, however, when injected had no influence on the color of a dark fish. Dark fins were cut from fishes, dipped immediately in boiling water to kill the skin in the dark phase and prevent

gradual blanching, and then extracted. These yielded the usual amount of residue, but this residue even at full strength failed to elicit any color change in pale pups. Such results show conclusively that the blanching produced by the extract from pale fins cannot result from a material extracted from the cartilage, muscle, blood, etc., in the fin but must come from that part of the fin concerned with the actual color change, for that part is the only one in which the pale and the dark fins differ.

During the season in which these tests were made the fins of about 150 smooth dogfishes were dried and extracted and the residues studied. Through the kindness of Dr. E. L. Martin of the Harvard Chemical Laboratory much of this material was subjected to chemical fractioning with the view of ascertaining, if possible, something of the nature of the concentrating neurohumor. Dried fins were sent from Woods Hole to Cambridge and were then pulverized and extracted in a Soxhlet apparatus with anhydrous, pure ether for 36 hours. The yellow ethereal extract thus obtained was put under reduced pressure for the evaporation of the ether and the resulting semi-solid, light-brown residue was sent to Woods Hole for testing. On injecting it into dark dogfishes it was found to excite the characteristic pale spots and it was thus shown to contain, as might have been expected, the concentrating neurohumor.

Further attempts were then made in Cambridge to ascertain something of the stability of the neurohumor concerned. Residues of the kind described were heated in a steam bath for ten minutes with four per cent sodium hydroxide. After extraction with ether and evaporation under a vacuum, the oily residue thus obtained was found to be fully effective in inducing pale spots in dark fishes. The alkaline fraction from this process was neutralized with hydrochloric acid, extracted with ether, washed with water, and dried. The slight residue thus obtained had no effect on the color of a dogfish into which it was injected.

A second extraction residue was washed three times with

two per cent sodium hydroxide then three times with two per cent hydrochloric acid and finally with water. On drying it with anhydrous sodium sulphate and extracting with ether a semi-solid material was obtained with a melting point between 80° and 100° C. When this material was injected under appropriate circumstances into a dark dogfish it was found to induce the formation of small, faint, pale spots. Purification by two additional ether extractions left the material still effective as a concentrating agent. The hydrochloric acid fraction from this test, after appropriate treatment and extraction with ether, yielded only an ineffective residue. In the course of these extractions a considerable amount of white flaky material was recovered which on purification showed the properties of cholesterol. When this substance was dissolved in olive oil and the mixture injected appropriately into dark dogfishes no pale spots appeared. Cholesterol apparently has no part in these reactions.

These tests, for which I am greatly indebted to Dr Martin, together with information already accumulated permit a certain rough description of the concentrating neurohumor to be made. It is a substance soluble in olive oil and in ether, but not in water. It can resist heat to 110° C. It is not decomposed by weak alkali nor by weak acid. It must therefore be regarded as a relatively stable compound. To hazard a guess as to its relation to other organic compounds would perhaps be premature, but its properties point to the possibility of its being one of the sterols, a class of bodies the significance of which in animal and plant activities is rapidly coming to be recognized (Fieser, 1936).

9 Discussion

The three selachians upon which the present paper is based possess melanophore systems which are in a measure individual. From the standpoint of color responses *Squalus* is relatively inactive, *Mustelus* and *Raja* active. In all three the dark phase is due to a neurohumor from the intermediate lobe of the pituitary gland. In *Mustelus* and in

Raja this hormone fluctuates with the state of the environment, but in *Squalus* there must be a fairly persistent flow of it irrespective of the surroundings thus keeping this dogfish more or less continuously dark. The pale phase in these fishes is more diverse. In *Mustelus* it is due to the direct action of concentrating nerves on the melanophores and very probably to nothing else. In *Squalus* some individuals apparently never blanch at all; others blanch slightly as a result of direct nerve action. In *Raja* blanching is unassociated with nerves and with neurohumors. It appears to be due to the absence of the dispersing hormone and to no other condition. These summarizing statements indicate how diverse the melanophore systems of these three elasmobranchs are.

In the so-called active members of the group, *Mustelus* and *Raja*, the change from pale to dark and the reverse require hours or even days for full completion. Such changes cannot be regarded therefore as effective means of adapting these fishes to their surroundings. At best they fit these forms to the general tone of their environment without meeting the details of such a setting quickly and accurately as, for instance, the chromatophore systems of many flatfishes do. This sluggishness reflects the general character of a system built on the basis of water-soluble neurohumors, the hydrohumors, as contrasted with one which is more predominantly nervous and acts through immediately applicable lipohumors. These distinctions have already been indicated by Hogben (1936) in his brief allusions to the temporal phase of this subject.

In many respects, however, Hogben's view (1936) of the plan of action in melanophore systems is strangely at variance with much that has been recently discovered in this field. His statement that it is now firmly established that the coordination of chromatic response in reptiles is due to the direct innervation of their pigmentary effector organs ignores completely the important part played by the pituitary secretion in, for instance, *Hemidactylus* (Noble and Bradley,

1933) and *Anolis* (Kleinholz, 1935). And further his declaration that the color changes in elasmobranchs are under endocrine control and that peripheral innervation is intrinsically improbable in this group also ignores the nerve control that was shown some years ago to be present in *Mustelus*. It is unfortunate for Hogben's general statements that they should thus omit a consideration of contrary observations by reputable workers made in advance of his own publication.

His difficulties however are not only due to his ignoring of sound evidence; they result primarily from his insistence on a distinction in melanophore research that is rapidly disappearing. A decade ago it was usual to ascribe chromatophore control to either a nervous or a humoral agent. This attitude was in large part the outcome of Hogben's own work and was a very important step forward. But the investigations of the last few years have made it progressively clear that this distinction is no longer valid. The excitation of chromatophores by nerves is due to activating substances given out by the nerves themselves, the excitation by hormones is caused by materials from distant endocrine glands brought to the chromatophores by the blood. In fact in some forms as, for instance, in *Ameiurus* the animal responds because both these influences work together: the action of a dispersing neurohumor from the adjacent nerves and that of another dispersing neurohumor carried from the distant pituitary gland to the color cells. In a word there is no real distinction between these two methods of excitation. In both, neurohumors are the effective agents; the question involved is merely one of the nearness or remoteness of the source (Parker, 1932, 1936d). From this standpoint the distinction of a nervous and a humoral excitation really vanishes and in consequence the question discussed by Hogben as to which of these two is the more primitive loses much of its meaning.

When the vertebrate melanophore system or better the chromatophore system as a whole, is regarded in the way just outlined, a new light is thrown on its operations. The

numerous neurohumors involved in color responses may be active in different species in such a variety of ways, singly or in combination, that an understanding is at once accorded to such differences as have been described in, for instance, the three elasmobranchs discussed in the present paper. Differences of this kind are not only thus apprehensible but are to be expected in animals the color changes of which are being studied. Notwithstanding the diversity which a conception such as this involves, the view here presented rests upon a reasonably unified basis which in the end is the application of the neurohumoral hypothesis to chromatophoral relations

10 SUMMARY

1. *Squalus acanthias* is a dark dogfish that shows little or no evidence of a pale phase. As it blanches somewhat on loss of its pituitary gland its general darkness indicates a certain continuity of pituitary secretion independent of its environment.

2. *Mustelus canis* and *Raja erinacea* show well marked dark and pale phases in response to changes in their surroundings.

3. The dark phase in these three elasmobranchs is due to a hydrohumor from the intermediate lobe of the pituitary gland whence it is carried in the blood to the melanophores. This substance, contained in commercial pituitrin and in intermedin, is different from the oxytocic and the pressor principles from the pituitary gland.

4. The pale phase in these fishes is due to the absence from the blood of any dispersing factor (*Raja erinacea*), or to the action of nerves (*Mustelus canis* and *Squalus acanthias* in part). In these elasmobranchs there is no evidence of a concentrating neurohumor such as the W substance (Hogben) believed to occur in *Scyllium* and in some species of *Raja*.

5. Adrenalin blanches *Mustelus canis*, *Squalus acanthias*, and *Raja erinacea* but probably plays no part in the natural paling of these fishes.

6. The pinkness of pale elasmobranchs may be as much

due to the exposure of the dermal blood-vessel by pigment concentration as to the absence of a pressor factor

7. The concentrating neurohumor in such elasmobranchs as *Mustelus* and *Squalus* is not carried by the blood; it is a lipohumor. It is soluble in olive oil, in ether, but not in water. It resists heat to 110° C., the action of sodium hydroxide and of hydrochloric acid. It is a relatively stable compound, possibly a sterol, but it is not cholesterol.

8. The color changes in elasmobranchs are slow in accomplishment involving hours and days, a condition associated with their usual means of excitation, chiefly hydrohumors.

9. In experimental operations on cold-blooded animals a mixture of broken ice and seawater or freshwater is a better means of stupefaction than drugs. Recovery from cold is more immediate and complete than recovery from drugs.

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LAND AND FRESHWATER MOLLUSKS FROM THE ISLAND OF COZUMEL, MEXICO, AND THEIR BEARING ON THE GEOLOGICAL HISTORY OF THE REGION

HORACE G. RICHARDS

(Read November 27, 1936)

ABSTRACT

The island of Cozumel lies in the Caribbean Sea about sixteen miles off the east coast of the Yucatan Peninsula. In order to study the molluscan fauna of this island and to obtain data on the relationship of this fauna to those of adjacent regions, a visit was paid to the island in April, 1936. Twenty-two species of land and freshwater mollusks were collected, of which four are described as new. With the exception of two or three species of widespread distribution throughout tropical America, and one previously reported only from Arizona, all the Cozumel species are intimately related to Yucatan and Central American forms. None are distinctly Cuban. The study of this fauna does not favor a geologically recent land connection between Cuba and Yucatan, but suggests that those species that do show some West Indian relationship reached Central America in early Tertiary time by a Jamaica-Honduras-Nicaragua land bridge. If there were no land bridge between Cuba and Yucatan at any time during the Pleistocene, as appears to be indicated by the mollusks, there may be some doubt cast on the theories recently advocated of a Pleistocene sinking of sea level of the magnitude of several thousand feet.

THE island of Cozumel lies between 20° and 21° north latitude and at 87° west longitude and about 16 miles off the east coast of Yucatan. It is a low limestone island approximately twenty-five miles long and ten miles wide, none of which is more than 30 feet above sea level. The island is densely covered with a low thick jungle or bush. Except for very small settlements or "ranchos," the only habitation is San Miguel, a town of about 2000 situated on the west shore of the island. Cozumel is part of the Mexican Territory of Quintana Roo.

Except for a single shell of the Tree Snail, *Liguus fasciatus* Muller collected by Dr. C. F. Millsbaugh in 1899, nothing has been known concerning the molluscan fauna of the island.

Mollusks have been collected at various times from the mainland of Yucatan, and several studies of the fauna have appeared, the most significant being that of Pilsbry (1892),

who studied the mollusks collected by an expedition led by Professor Angelo Heilprin, and the more recent papers of Bequaert and Clench (1933, 1936)

Until a few years ago it was very difficult to reach Cozumel, there being only very irregular boat service from Progreso or Belize. However in 1929 the Pan American Airways System established a refueling station at Laguna Ciega, on the north end of the island, and at the present time planes stop at Cozumel once a week in each direction on the Miami-Havana-Merida flight

Because of its position between Cuba and Yucatan and the possible bearing of a study of its fauna on problems of paleogeography, it appeared desirable to obtain a collection of mollusks from Cozumel. With the aid of a grant from the Penrose Fund of the American Philosophical Society, I was able to spend a week collecting mollusks on this island. I arrived at Cozumel on the afternoon of April 17, 1936, after a three and one-half hour flight from Havana, Cuba. During the week on the island, I collected mollusks from numerous localities mostly on the west side of the island near San Miguel

Nowhere were mollusks exceptionally abundant. This was probably due in part to the fact that it was still the dry season; but even dead shells were scarce, and it seems probable that the fauna of the island is comparatively small. *Helicina arenicola* (Morelet) and *Choanopoma cozumelensis* Richards were probably the most abundant snails. *Drymaeus shattucki cozumelensis* Richards was often seen crawling among the leaves and low bushes along the trails.

The thick growth of the jungle and the scarcity of trails made it impossible to cover as much of the island as might have been desired. However with the aid of a Maya Indian guide, I visited some ruins of ancient Maya temples near Santa Rita and San Gerbacio, near the center of the island, numerous mollusks were found on this trip. Mollusks were especially abundant near the ruins of the old Spanish Church (built about 1519) and nearby a dried swamp yielded some

dead shells of *Planorbis orbiculatus* Morelet, *P. cultratus* Orbigny and *Succinea carmenensis* F & C

On the morning of April 25 (half a day late) I left the lagoon at Cozumel and after a fascinating two and one-half hour trip over thick jungles and chicle forests, I arrived at the airport in Merida, the capital of the state of Yucatan. While in Yucatan I was able to make a small collection of mollusks near some of the Maya ruins at Chichen Itza. This material has proved valuable for comparison with the mollusks from Cozumel.

In all, 22 species were collected from the island of Cozumel, of which 4 are new. Certain of these species were also found at Chichen Itza, other species found at Chichen Itza were not found at Cozumel. A list of the mollusks collected at Chichen Itza will be found at the conclusion of the discussion of the fauna of Cozumel (p. 257).

ACKNOWLEDGMENTS

I wish to express my thanks to the American Philosophical Society for the grant from the Penrose Fund which made possible the visit to the island of Cozumel. I also wish to express my gratitude to Dr. H. A. Pilsbry, of the Academy of Natural Sciences of Philadelphia, who has given considerable assistance in the study of the material and who has verified all the identifications.

A set of the mollusks has been deposited in the Academy of Natural Sciences.

LAND AND FRESHWATER MOLLUSKS FROM COZUMEL

Oleacinidae

Euglandina cylindracea (Phillips)

One broken shell from near San Miguel. This species is very variable. The true *cylindracea* together with the elongate variety (*E. yucatanensis* (Pfeiffer)) were found to be common at Chichen Itza, and are reported from other places in Yucatan.

Streptostyla pilsbryi new species (Plate IV, Fig. 2)

Shell ovate oblong, somewhat solid and glossy, translucent, deep colonial buff with a slight orange tinge, whorls 5, apex blunt, columellar fold weak Length 10.7 mm., width 4.6 mm., length of aperture 7.2 mm

This species is about the size of *S. meridina* (Morelet) but distinguished from it by its blunter apex and far weaker columellar fold

The type (A.N.S.P. 167748) and six other shells were taken near the ruins of San Gerbacio, Cozumel Island

This species is apparently closely related to *S. meridina* (Morelet) and *S. ventricosula* (Morelet), both of which occur on the mainland of Yucatan.

Named in honor of Dr. Pilsbry, who has generously given considerable assistance in the preparation of this paper

Zonitida

Guppya gundlachi (Pfeiffer)

Near San Miguel, Cozumel. This species is rather widely distributed throughout southern Mexico, Central America and the West Indies.

Sagdidæ

Thysanophora cæcoides (Tate)

Near San Miguel, Cozumel. This species is widely distributed throughout Yucatan and Central America

Thysanophora plagiptycha (Shuttleworth)

With the above. Of widespread distribution in Central America and the West Indies. Also known from the Swan Islands (Pilsbry, 1930, p. 241).

Fruticicolida

Averelia (Trichodiscina) coactiliata Deshayes

About 3 miles north of San Miguel. This species is a common Central American form and is known from Vera Cruz to Panama.

*Bulimulidae**Drymaeus shattucki* Bequaert and Clench

Near San Miguel, Cozumel. Bequaert and Clench described this species from Chichen Itza, Yucatan, and it is also known from Tabi and Progreso

Drymaeus shattucki cozumelensis new variety

(Plate IV, Fig 4)

The shell resembles the typical *shattucki* except that the color is white with the tips of the apex, the umbilical area and the columella, coral pink

Length 28.9 mm.; width 13.2 mm., length of aperture 13.0 mm.

Abundant living among the leaves and low bushes on the trail from San Miguel to Santa Rita, Cozumel (Type A.N.S P 167744)

Although color is often a variable factor in *Drymaeus*, it has been thought worth while to call attention to this island form since the thirty-five examples collected all have the same pattern. So far as existing specimens and records go, this pattern has not been found to occur on the Yucatan mainland.

A single shell was found which was barium yellow in color with the same coral pink markings.

Oxystyla princeps (Sowerby)

A few dead shells were found near the beach on the west side of Cozumel Island. This is a common arboreal species of southern Mexico and Central America.

Bulimulus sanmiguelensis new species (Plate IV, Fig 6)

The shell is thin, ovate-conic, corneous brown with slight irregular growth wrinkles of the spire, stronger on the last whorl, whorls $5\frac{1}{2}$, very slightly convex, sutures superficial. Apex blunt, the embryonic whorls with crinkled and anastomosing microscopic wrinkles. Peristome thin and simple, the columellar margin reflected.

Length 18 mm., width 9.1 mm.; length of aperture 9.4 mm.

The type (A.N.S.P. 167746) and eight other specimens were collected near the town of San Miguel, Cozumel.

This species resembles *B. unicolor* (Sowerby) in general appearance, but is distinguished from it and allied forms by the nearly flat whorls of the spire which are united by relatively superficial sutures

Urocoptidae

Brachypodella speluncae (Pfeiffer)

A small form of which no perfect shells were found. A specimen of eight whorls measured 8.3 mm long. The ribs are somewhat more widely spaced than in the typical form. Found near the ruins of San Gerbacio and near the town of San Miguel. The species is known from Yucatan and Guatemala.

Microceramus concisus (Morelet)

Near ruins of the church (1 mile from San Miguel) and at San Gerbacio. The species is known from Yucatan, Guatemala, Swan and St. Andrews Islands.

M. concisus (Morelet) is apparently closely related to *M. gossei* (Pfeiffer) from Jamaica.

Subulinidae

Lamilaxis micra (d'Orbigny)

San Gerbacio, Cozumel. This species, frequently referred to the genus *Opeas*, is of wide distribution throughout all of tropical America and its range has probably been considerably extended by accidental introduction.

Lamilaxis martensi (Pfeiffer) (Plate IV, Fig. 1)

Near San Miguel and the ruins of San Gerbacio. This species has been referred to the genus *Leptinaria* in the literature.

Some of the shells from Cozumel are larger than the usual Mexican specimens of *L. martensi*, one shell from Cozumel reaches a length of 11 mm. and a width of 5.4 mm. ♀

The species is known from the mainland of Mexico and Yucatan.

(Figured specimen A.N.S.P. 167147.)

Succineidae

Succinea carmenensis Fisher and Crosse (Plate IV, Fig 5)

The dead shells of this species were common in a dried swamp a few miles north of the town of San Miguel. The shells from Cozumel run considerably larger than the typical *carmenensis*, reaching a length of 17.5 mm.

Described from the island of Carmen and also known from Chichen Itza, and Santa Ana, near Calcehtok in Yucatan.

(Figured specimen A.N.S.P. 167745)

Planorbidae

Planorbis orbiculus Morelet

Shells abundant in a dried swamp a few miles north of San Miguel, also in a similar swamp near San Gerbacio. The species is apparently identical with *P. liebmanii* Dunker and is known from Vera Cruz, Yucatan and Guatemala.

Drepanotrema cultratum d'Orbigny

Several young shells were found associated with the above in the dried swamp a few miles north of San Miguel. The species with several varieties is known from southern Mexico, Central America, the northern part of South America as well as some of the Lesser Antilles.

Planorbula obstructa (Morelet)

With the above two species a few miles north of San Miguel.

A species of wide distribution in Central America, Yucatan, Mexico and South Texas.

Gyraulus arizonensis Pilsbry and Ferriss

With the above three species in the dried swamp near San Miguel, also near San Gerbacio.

This species was described from the San Pedro River in Arizona, and has hitherto been known only from that vicinity. Its presence on Cozumel is certainly surprising.

*Physidæ**Aplexa spiculata* (Morelet)

San Gerbacio, Cozumel.

This species has been reported from the mainland of Yucatan and Vera Cruz

*Pomatiasidæ**Choanopoma cozumelensis* new species (Plate IV, Fig. 3)

The shell is narrowly umbilicate, elongate conic, truncate. The $3\frac{1}{2}$ whorls retained are strongly convex, the embryonic whorls usually lost. Light brown with paler riblets, spiral series of sparse, unequal chestnut-brown dots are strongly developed on the two lower whorls, fainter on the upper whorls. Sculpture of fine, close, nearly regular axial riblets about 9 in 1 mm on the last whorl, decidedly more widely spaced on the upper whorl retained, groups of two to three riblets project inconspicuously at the suture. Spiral sculpture developed only in the umbilical area, where there are several (4 to 6) coarse spiral cords. Aperture nearly circular. The flatly reflected peristome is widened at the posterior angle and slightly so at the columellar margin also, where it shows faint traces of fluting.

Length 9.7 mm; width 7.0 mm; length of aperture with peristome 7.0 mm.

Operculum white with gray nucleus above the lower third of the length, the last whorl with fine, somewhat irregular retractive striæ.

Type (A N S.P. 167749) from San Gerbacio, Cozumel, the species was also found near San Miguel, abundant at both localities.

This species closely resembles *C. andrewsæ* (Ancey) from Utila Island, off the east coast of Honduras, but is distinguished from it by the chestnut dotted bands, its slightly more convex whorls and especially by its sculpture which is finer than in *andrewsæ*.

*Helicinida**Helicina arenicola* Morelet

Common near the ruins of the church near San Miguel and near San Gerbacio.

This is the first record for the species outside of the state of Yucatan

One shell of *Liguus fasciatus* Muller is in the Field Museum at Chicago (catalogue number 8832) said to have been collected by Dr C F Millspaugh from a sabal palm near the beach at Cozumel on February 18, 1899 (See Pilsbry, 1899, p 170) The presence of this species on Cozumel was not verified on the recent trip, and it seems possible that the one shell collected by Dr Millspaugh was an accidental introduction, probably from Cuba

MOLLUSKS COLLECTED FROM CHICHEN ITZA, YUCATAN

Streptostyla meridina Morelet*Streptostyla ventricosula* Morelet*Euglandina cylindracea* (Phillips)

(*E yucatanensis* Pfeiffer)

Microceramus concisus (Morelet)*Bulimulus unicolor* (Sowerby)*Drymaeus serperastrum* (Say)*Oxystyla princeps* (Sowerby)*Cacilioides consobrina prima* De Folin

(A Central American form not previously reported from Yucatan)

Poteria berendti Pfeiffer*Lamilaxis micra* (d'Orbigny)

(*Opeas micra* d'Orb)

Choanopoma largillierii (Pfeiffer)*Choanopoma gagei* Bequaert and Clench*Helicina arenicola* (Morelet)

GEOLOGY

Probably the first to do any detailed work on the geology or paleontology of Yucatan was Heilprin (1891). He rec-

ognized limestone of both Pliocene and Pleistocene (Post-Pliocene) age, the latter occurring mostly along the coast.

Sapper (1896) prepared a geological map of Yucatan in which he recognized Pleistocene, Pliocene and other limestone of possible Pliocene or Miocene age. Later (1905) in mapping Yucatan and other parts of Central America, he says that Yucatan consists of only Pliocene and Pleistocene limestone.

Engerrand and Urbina (1910) discussed the geology and paleontology of the Yucatan Peninsula and mapped certain contacts between the Pliocene and Pleistocene. At El Cuyo, on the north coast of the state of Yucatan near the boundary of Quintana Roo, Engerrand and Urbina record a marine Pleistocene fauna. Their best collecting was in a limestone cave ("Sascaberas")

Nothing specific has been written on the geology of Cozumel. Sapper (1896) mapped the island as Pliocene. Limestone occurs almost everywhere on the island, but in few places is it fossiliferous. Along the shore near San Miguel some large fossils of *Strombus* cf. *gigas* and some unidentified pieces of coral were observed (Plate II)

Near the Rancho Santa Rita, near the center of the island, a small limestone cave was noted (Plate III). The roof of the cave had crumbled and numerous identifiable marine fossils were found on the floor of the cave. The following species have been identified.

(Gastropoda)

Bulla amygdala Dillwyn
Conus stearnsi Conrad
Conus mus Hwass
Conus verrucosus Hwass
Olivella nivea Gmelin
Marginella apicina Menke
Nassa vibex Say
Nassa ambigua Montfort
Cerithium floridanum Morch
Cerithium sp. (very worn)
Pyramidella dolabrata Linne

(Pelecypoda)

Arca occidentalis Philippi
Arca barbata Linne
Lucina jamaicensis Lamarck (?)
Cardium medium Linne
Chione cancellata Linne
Chione intapurpurea Conrad
Pitar cf. *simpsoni* Dall
Semele proficua Pulteney

Chione cancellata Linne and *Bulla amygdala* Dillwyn were especially abundant. All these species live in the Caribbean Sea to-day, and practically all are reported from the Pleistocene of Western Cuba (Richards, 1935), none are distinctly Pliocene. It therefore seems best to regard the deposit as Pleistocene, it is possible that there may be Pliocene rocks on the island, but the limestone seems rather uniform wherever exposed and it seems highly probable that the entire island is composed of Pleistocene rock. The cave near Santa Rita on Cozumel resembles in general appearance the picture of the cave near El Cuyo where Engerrand and Urbina listed the Pleistocene fossils.

PALEOGEOGRAPHY

Numerous paleogeographers have suggested a late Tertiary or even Quaternary land bridge between Yucatan and Western Cuba. Heilprin (1891), for instance, suggested a Quaternary connection. Schuchert (1910) in his series of paleogeographic maps shows a Pliocene land bridge between these two places and Vaughan (1918) suggests an upper Miocene connection.

More recently, however, Pilsbry (1930 p. 222) has pointed out that "it does not seem likely that there has been any direct connection between Cuba or Jamaica and any part of Yucatan or Central America later than Paleocene or Eocene."

In the paleogeographic maps of his recent excellent treatise on the Antillean-Caribbean region, Schuchert (1935) omits the Tertiary land bridge between Cuba and Yucatan, although the connection between Honduras-Nicaragua and Jamaica is shown existing as late as the Pliocene. In summarizing the evidence Schuchert says (pp. 107-8).

"Most zoogeographers see continental land contacts in two places: an older, greater, and longer enduring bridge from Honduras-Nicaragua across to Jamaica and Hispaniola, and a much younger, evanescent one from Yucatan to Cuba and Hispaniola. The writer does not see the evidence for this latter bridge. It appears to him that no bridge existed from Cuba to Yucatan after Triassic time, and more especially during the later Cenozoic, since the latter land was then widely beneath the sea, and as for Mesozoic connection, it also appears improbable for the same reason. The only

bridge that seems probable, from the geological evidence, is that from Honduras-Nicaragua to Jamaica and Hispaniola"¹

The above statement is more in accord with the views of Pilsbry cited above except that Schuchert extends the Honduras-Nicaragua-Jamaica land bridge until the end of the Tertiary, whereas Pilsbry says that it existed no later than the Eocene.

The land mollusks of Yucatan are almost entirely of Central American affinities and there is a conspicuous lack of West Indian groups. Those groups that do show a distant West Indian relationship (*Choanopoma*, *Brachypodella*, etc.) are more related to Jamaican forms and probably reached Central America in early Tertiary time by the land bridge to Honduras and Nicaragua. Since much of Yucatan was below water in later Tertiary and Quaternary time, most of its fauna must have been derived by geologically recent migration, thereby accounting for the comparative small fauna of the region. Bequaert and Clench have pointed out that if Yucatan had been joined to Cuba in the Pliocene or Pleistocene, there should now be some Cuban elements in its present fauna. The lack of these is a strong argument against such a connection.

The bird fauna of the island of Cozumel contains some decided West Indian affinities (Griscom, 1926) and the one mollusk previously reported (*Liguus fasciatus* Muller), the presence of which incidentally was not verified on this trip, is a Cuban and Florida species, not known from Yucatan or Central America. Therefore, the finding of a fauna of 22 species of land and freshwater mollusks, most of which are intimately related to Yucatan and Central American forms, and none closely related to Cuban species (except two or three of general distribution throughout the Antillean-Caribbean region) is highly interesting, and more in harmony with the other data on paleogeography, suggesting an early Tertiary land bridge from Jamaica to Honduras and Nicaragua rather than a connection from Cuba to Yucatan.

¹ Reprinted by permission from *Antillean-Caribbean Region* by Charles Schuchert, published by John Wiley & Sons, Inc.

PLEISTOCENE LOWERING OF SEA LEVEL

Most geologists agree that during the glacial stages of the Pleistocene, sea level was lowered due to the water removed from the sea to form the land ice. Conservative estimates of this lowering as given by Antevs (1928) and Daly (1929) are between 260 and 300 feet. The Yucatan Channel is in places 6000 feet deep, consequently a lowering of sea level of this magnitude would not have caused the joining of Cuba with Yucatan.

Recently Shepard (1936) has suggested the possibility of a much greater fall of sea level in order to account for the submarine valleys which he thinks were cut during the Pleistocene when sea level may have been several thousand feet lower than at present. Such a lowering of sea level would probably have joined Cuba with Yucatan, or at least made it possible for the migration of land forms from Cuba to Yucatan. The absence of Cuban elements in the molluscan fauna of Yucatan seems to cast some doubt on a Pleistocene lowering of sea level of any great magnitude.

It is possible that some of the Cuban forms might have been drowned out by a subsequent high sea level stage, for instance on Cozumel and along the coast of Yucatan, but they certainly should have persisted in the interior of Yucatan, which as far as we know was not covered by a Pleistocene sea.

SUMMARY

1 Twenty-two species of land and freshwater mollusks were found on the island of Cozumel, of which four are described as new.

2 With the exception of two or three species of widespread distribution throughout tropical America, and one previously reported only from Arizona, all the Cozumel species are intimately related to Yucatan and Central American forms.

3. A small collection of thirteen species from Chichen Itza, Yucatan, is recorded, including one species not previously reported from Yucatan.

4. Pleistocene marine fossils are recorded from a cave on Cozumel Island.

5 The study of the fauna does not favor a geologically recent connection between Cuba and Yucatan, but suggests that those species that do show some West Indian relationship reached Central America in early Tertiary time by a Jamaica-Honduras-Nicaragua land bridge.

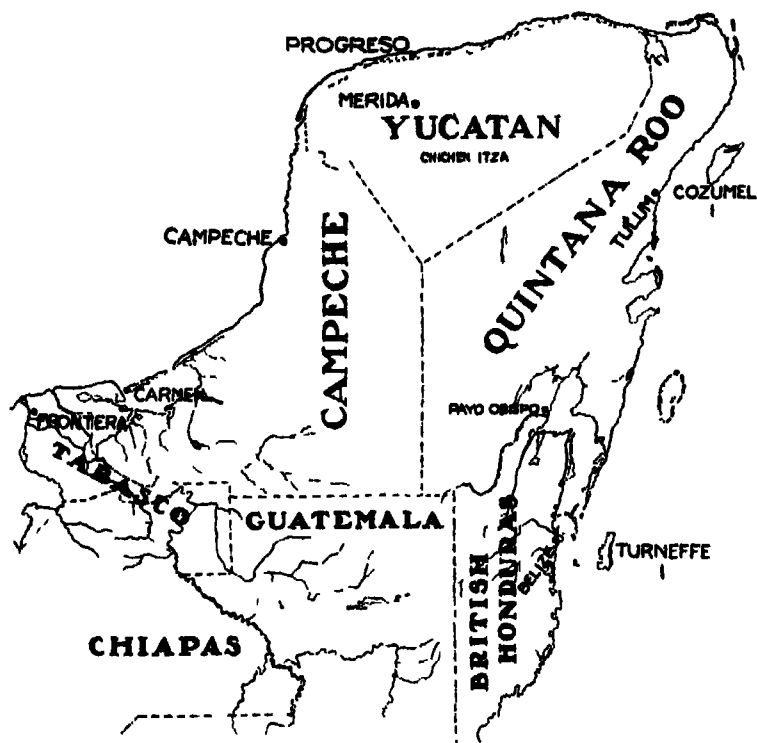
6 If there were no land bridge between Cuba and Yucatan at any time during the Pleistocene, as appears to be indicated by the mollusks, there seems to be some doubt cast upon the theories recently advocated of a Pleistocene sinking of sea level of the magnitude of several thousand feet

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PLATE I



Map of Yucatan Peninsula showing Cozumel Island

PLATE II



FIG. 1 Beach of Cozumel Island north of San Miguel



FIG. 2 Pleistocene (?) limestone near San Miguel

PLATE III



FIG. 1. Cave near Santa Rita

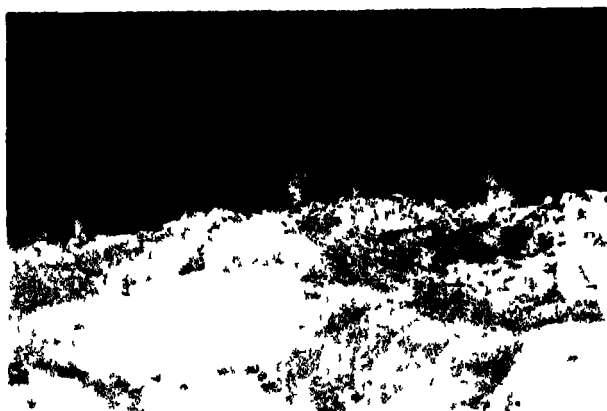


FIG. 2. Interior of cave near Santa Rita

PLATE IV

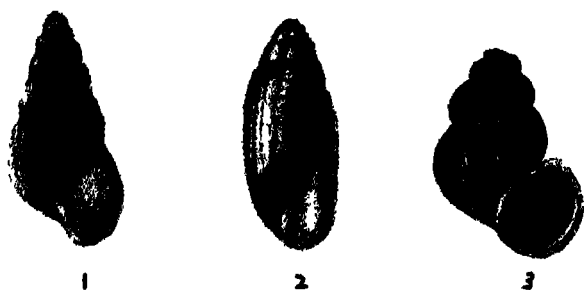


FIG 1 *Iamularia martensi* (Pfeiffer) $\times 3$
 FIG 2 *Streptostyla pulchra* Richards (type) $\times 3$
 FIG 3 *Choanopoma cozumelensis* Richards (type) $\times 3$

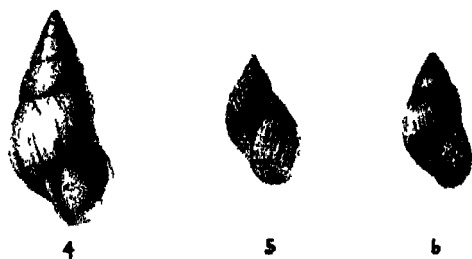


FIG 4 *Drymaeus shattucki cozumelensis* Richards (type) $\times 1$
 FIG 5 *Succinea carmenensis* F. & C. $\times 1$
 FIG 6 *Bulimulus sanmiguelensis* Richards (type) $\times 1$

THE STRUCTURE AND FUNCTION OF THE FACIAL AND LABIAL PITS OF SNAKES *

G K NOBLE AND A. SCHMIDT

ABSTRACT

The New World vipers, Crotalidæ, are distinguished from all other snakes by a sensory pit on each side of the face. Some Boidæ have a series of sensory pits on the scales of their upper and lower jaws. Experiments have shown that both types of pit serve to detect the body temperature of the snakes' prey. In the more primitive boids the pits are purely temperature discriminating mechanisms, but in the crotalids they have the additional function of detecting air vibrations.

The snakes can invariably distinguish between covered electric light bulbs, one warm and one cold, when moved synchronously on a mechanical arm at distances where the temperature gradient produced by the warm bulb is only two-tenths of a degree Centigrade or less above that of the environment. When all the sensory mechanisms of the head except the pits are prevented from functioning the snakes are still able to distinguish between the bulbs.

In the absence of vision, pit vipers respond more consistently to the warmth of the prey's body than to its movements. In both the boids with labial pits and in the pit vipers the odor of the prey evokes tongue flicking while the temperature gradient from the prey's body calls forth the strike. In the absence of vision the labial and facial pits are the most important sensory mechanisms for directing the strike towards warm blooded prey.

Both labial and facial pits are innervated by the fifth cranial nerve and in both the nerve terminations are knob-like enlargements lying between the unspecialized cells of the epidermis. Facial pits differ from labial pits in having a membrane stretched across their bottoms. The ontogeny indicates that the facial pit was evolved by the partial fusion of two pits of the type found on the lips of boids. The intervening wall between the pits remains as a drum head, the facial pit membrane.

THE "pit vipers," or Crotalidæ, include the common poisonous snakes of the New World such as the rattlesnakes, moccasins and copperheads. The group is distinguished from the viperid snakes by the presence of a pit on each side of the face between the nostril and eye. This pit has been variously described as an auditory organ, a tear sac, a duct giving air access to the poison, a gland, an organ of a sixth sense, a tactile organ, a tegumental sense organ of the lateral line series, and a chemical sense organ allied to olfaction and gustation. It has been known since 1824 that the pit is

* These studies have been aided by a grant from the Josiah Macy, Jr., Foundation

richly supplied with nerves. As long ago as 1900 West figured nerve "terminations" in the membrane which stretches across the bottom of each pit. More recently Lynn (1931) has figured similar terminations in another species of pit viper. He concludes in part

"In its structure the organ under consideration shows certain very striking resemblances to the chordotonal organ of insects, an organ which is known to be auditory in function. The pit organ, it would seem, is structurally well adapted to perform a similar function. It is innervated by a nerve which, in other snakes is known to supply tactile end organs. The pit organ may represent a concentration of that function."

In reaching this conclusion Lynn refers to some earlier work of one of us (Noble, 1930) which seemed to indicate a tactile function for the facial pit. These experiments were summarized later (Noble, 1934) as follows.

"Experiments with blindfolded, nose-plugged and tongueless moccasins and rattlers reveal that these snakes will strike in the direction of gusts of air. Elimination of the facial pit reduces this ability. The facial pit membrane may be considered a modification of the integument of the head which aids the detection of air vibrations."

This conclusion seemed to receive support in the fact that the nerve terminations described by one of us were not cells such as West (*loc. cit.*) and Lynn (*loc. cit.*) reported but small knob-like enlargements similar to those found in the unspecialized integument of the head. Such terminations are especially abundant on the papilla-like structures of the epidermis of the lips and these have been considered by Jaburek (1927) and other students to be tactile organs. Many crotalid snakes are crepuscular or nocturnal and it would seem that sensitive tactile organs would aid them in orienting their strike.

The chief objection to this conclusion was that small air disturbances of the same magnitude as those made by the movements of a rodent usually brought forth no response in a pit viper deprived of visual, olfactory and Jacobson's organs.

The facial pits, if tactile organs at all, seemed to respond only to coarser air movements.

Very recently Ros (1935) has experimented with a single specimen of *Python seba*, a species which like most other pythons is equipped with a series of labial pits. Lynn (*loc. cit*) compared these with the facial pits of Crotalidæ and concluded that "although they are innervated by the same nerves as are the facial pits of the pit vipers, they have been found to differ markedly from the latter with respect to form and cellular structure, and the indication is that the two are in no way homologous." Nevertheless Ros secured some evidence that her snake responded to air vibrations produced by a vibrating wire. Since it was attracted by warmth, and less effectively when its pits were filled with vaseline, paraffin or wax, Ros concluded that the pits were sensitive to heat waves. Other snakes are also attracted to warm areas. Some species, such as *Storeria dekayi*, which lack pits are very sensitive (Noble and Clausen, 1936). Ros did not show that her Python responded differently from a pit-less species in the same situation. Still her suggestion that pythons may be sensitive to the heat of their prey seemed worthy of further investigation. We have therefore begun a study of the reaction of snakes to objects of different temperatures. By utilizing different methods than Ros employed we were able to eliminate completely the odor of prey. Although no series of pythons were available to us we have employed a large group of boids having labial pits also many species of crotalid snakes.

MATERIAL AND METHODS

At the outset of our work it was discovered that both *Boa hortulana* and the crotalid snakes could readily distinguish between a warm and a cold electric light bulb when these were covered with cloth and moved before them. In order to have a uniform series of conditions throughout our tests, it was found necessary to suspend the bulbs on a horizontal rod which was attached to a large fly wheel on a motor. Rheostatic control made it possible to move the bulbs at a

wide range of speeds. Since the relative positions of the cold and warm bulbs were changed at nearly every trial, the danger of training the snakes to place habits was avoided. The bulbs were covered either with rubber cloth, or felt and linen cloth tightly bound with adhesive tape. These wrappings were frequently changed and in every case the shape of the cover made as nearly as possible identical to that on the other bulb. Each bulb was suspended from the movable rod on a stiff wire 200 mm in length. A movable platform for the test snakes was placed in front of the bulbs and the whole apparatus installed in a large box in a dark room. A shielded light illuminated only the bulbs and platform. The observer was further screened by the walls of the box.

In certain experiments an eight inch electric fan was employed to modify the air currents. In others freshly killed rats were attached to the bulbs. The apparatus was arranged in such a way that the pair of bulbs could be removed and swung by hand. This permitted a wide variety of irregular movements. Results secured from this method of stimulation were compared with the results obtained with the bulbs attached to the moving rod of the motor.

Finally a detailed histological check was made of the pits of the snakes employed in these experiments. The preparations were supplemented by others which formed the basis of a previous report (Noble, 1934). Some years ago, Dr F. B. Manning began a detailed histological study of the facial pit of crotalid snakes. After his untimely death Dr Thomas Barbour entrusted one of us with Dr Manning's slides and notes for further study. These notes did not give us a clue as to what conclusions Dr Manning may have reached. Some of his drawings published as part of this report indicate that he well understood the general morphology and development of the pit. Additional slides of the facial pit of a crotalid snake were loaned us by Prof. Leon J. Cole. In the course of our histological studies we have received technical assistance from Drs Ludwig Hirning and George F. Laidlaw. We are especially indebted to Mrs. Priscilla Ryan for aid throughout the course of this study.

TEMPERATURE DISCRIMINATION

Temperatures were recorded with mercury thermometers. For all readings a highly sensitive thermometer with a bulb 7×2 mm. was employed in combination with a precision thermometer graduated to 0.1°C . The thermometers were mounted on stands and moved without touching them in order to avoid slight fluctuations due to the proximity of the observer.

A 25-watt bulb was wrapped in one thickness of felt cloth, then two thicknesses of linen and bound with adhesive tape for utilization in the apparatus described above. The wrapped bulb was tested at frequent intervals throughout the course of the experiments. On no occasion would it influence the thermometers when they were placed at a distance greater than 25 cm. For example, on one occasion when the experimental platform registered 26.4°C . the surface of the bulb was 69°C . At 5 cm. distance the thermometers registered 32°C ., at 10 cm. 28.2° , at 15 cm. 27.2° , at 20 cm. 26.6° , at 25 cm. and beyond 26.4°C .

When on the same occasion the same bulb was moved in the apparatus, at the rate of fifty passes (twenty-five double swings) a minute in front of the platform a temperature difference was first recorded at 15 cm. At 10 cm. distance the temperature was 27.4°C ., at 5 cm. 29.2° . The temperature varied with the speed of movement of the bulb but forty passes a minute was considered the standard speed because it brought the maximum response from the snakes. At this speed no difference between the temperature of a wrapped heated bulb and of an unheated one could be detected at distances greater than 16 cm.

EXPERIMENTS WITH *BOA HORTULANA*

Eight adult *Boa hortulana* were tested in the above apparatus as well as a series of ten recently born individuals of the same species. These snakes were very uniform in their responses. All the snakes were tested in the apparatus and several at frequent intervals.

The warm or cold bulbs when brought slowly toward a *B. hortulana* will induce little or no response. When the bulbs are moved in the apparatus at speeds greater than fifty passes a minute the snakes are usually frightened and either endeavor to escape or strike viciously in the direction of either bulb. For the adult snakes the strike usually occurs first at a distance of 32 to 35 cm and the blow often falls between the two bulbs. When the snakes are blindfolded by covering the eyes with adhesive tape pads slightly larger than the orbits and painted black with India ink, they will invariably distinguish between the bulbs. They will strike at the warm bulb at distances of 16, 18 and 25 cm. As pointed out above, the temperature difference between the bulbs at this distance is 0.2° C. or less, the mercury thermometers being inadequate for recording temperature difference at greater distances. Individuals varied greatly in their ability to discriminate at distances over 30 cm. The best record made by any of the eighteen snakes was perfect discrimination at 48.5 cm. This record was made by an adult which had just finished shedding and had not been previously tested in the apparatus. Many blindfolded boas showed an obvious interest in the warm swinging bulb when over 40 cm. away but did not strike until it was brought 37, 34 or fewer centimeters from them.

In order to determine the sensory mechanism employed in this very fine temperature discrimination, the various sense organs were eliminated in turn, the snakes being tested after each change. Plugging the nostrils with cotton soaked in a ten per cent solution of collodion has no effect on their ability to discriminate. Removing the tongue has also no effect. Tests were made immediately after both operations and also several days later. In the case of tongue removal there is a period approximately half an hour after the operation until two days later during which the snakes fail to respond to either bulb. This probably is caused by the pain of the tongue stub. The removal of the tongue prevents the functioning of Jacobson's organ, a mechanism which plays an

important rôle in the life of most snakes (Noble and Clausen, *loc. cit.*).

Covering the entire upper surfaces and sides of a boa's head with adhesive tape leaving only the pits on upper and lower labial shields exposed does not seriously affect the temperature discrimination of the snakes. In strong contrast merely filling the pits with a ten per cent solution of collodion stops the blindfolded snakes from striking at the swinging bulbs. Removing the collodion restores immediately the response and ability to discriminate. If the pits on one side of the head are closed with collodion and the bulbs swung at the usual distance of 16 to 25 cm. from that side of the head there is no response but the snake strikes at once when the warm bulb is swung over to the other side of the head.

A warm bulb brought slowly towards the blindfolded and pit-filled snake evokes no strike. If the bulb is moved at a few centimeters' distance above the head or even above the right or left side it calls forth no movement of head or tongue. But when the same bulb is dropped down to a position in front of the snout there is induced a pronounced flickering of the tongue and often a turning of the head in the direction of the bulb. If the pits are adequately sealed this movement of the warm bulb never induces a strike. It is obvious, however, that the rostral portion of the head is sensitive to marked temperature gradients such as are induced by the warm bulb at 5 cm. distance.

Warmth without movement will not evoke a strike from the blindfolded snake. Jets of warm air produced by turning on a fan or a compressed air line behind a stationary bulb will also have no effect. When these air currents are vibrated at approximately forty movements a minute there is still no response if the warm bulb itself remains stationary. Making and breaking the current to the stationary bulb are also without effect upon the snake.

Greatly increasing the temperature by adding bulbs of higher wattage does not lengthen the striking distance in a definite manner. At least no snake exceeded the maximum

record made with the 25 watt bulb. When the hot bulbs were brought near, the snakes being tested veered away. Placing a fan at right angles to the moving bulbs cuts down the distance at which discrimination can be made but it does not destroy discrimination entirely. The vibration of the fan tends to distract the snakes and this may contribute to their failure to discriminate at longer ranges.

Snakes were tested for a five-minute period in each experiment. The number of strikes and the distance of the snake at the moment of striking were recorded to the nearest centimeter. Two protocols will illustrate the method.

Boa 4, Apr 30, blindfolded with standard pads, distinguishes between warm and cold bulb 4 times in standard period, distances at moment of strike 17, 16, 14 and 13 cm respectively.

Pits closed with collodion at 10.45 A.M. No strikes could be induced at noon or at 1.20 P.M. At 1.45 collodion removed. Five strikes at warm bulb induced with standard apparatus during next 5 minutes; distances 16, 18, 15, 16 and 13 cm. respectively.

Tongue removed, snake tested with standard apparatus strikes at warm bulb at 16, 14 and 13 cm. respectively during standard period.

May 4, Boa 4, blindfolded and tested again, strikes at warm bulb at 16, 16, 18, 12 and 15 cm. respectively during 5 minute period. Nostrils plugged with collodion and cotton. Snake strikes at warm bulb at 16, 18, 16, 16 and 22 cm respectively during same period.

Boa 5, May 1, blindfolded snake, strikes at warm bulb 3 times during standard period, distances 18, 16 and 14 cm. respectively. Nostrils plugged with collodion and cotton, entire upper surface and sides of head covered with adhesive tape leaving only the pits free. Snake strikes at warm bulb 4 times during standard period, distances 16, 16, 18 and 20 cm. respectively. At 1.20 P.M. tongue removed. Snake strikes 7 times during standard period, distances 16, 18, 15, 18, 20, 16 and 17 cm. respectively. Tests repeated at 2.10, 3.00 and 3.30 P.M. without inducing a strike.

May 4. Same snake blindfolded, with nostrils plugged and tongue removed, strikes at warm bulb 3 times during standard period, distances 16, 17 and 18 cm. respectively

Blindfolding makes the striking of any particular snake more uniform. A snake if nervous would usually strike at greater distances if vision was unimpaired. In some cases the sight of the experimental equipment inhibited the striking behavior of a snake and blindfolding served to release the characteristic response. Thus in one series of tests with adult snakes neither No 7 nor No 8 would strike at the bulb before being blindfolded while after the pads were adjusted over their eyes, No 7 struck at 24 cm. distance at the warm bulb and No 8 at 18 cm. Snake No. 2 struck at both bulbs when 30 cm. away. After blindfolding it selected the warm bulb consistently at a distance of 41 cm. Further, No 1 struck in the direction of the moving bulbs when they were 33 cm. distant, but when blindfolded selected only the warm bulb when it was moved to the 22 cm. mark. Similarly No 3 struck at 32 cm. before blindfolding, and 28 cm. after the operation, No. 4 at 25 cm. before and 21 after, No. 5 at 52 cm. before and 38 after, No 6 at 42 cm. before and 27 after.

There was considerable variation in the reaction of any one snake from day to day. Thus No. 2 which in the above experiments was inhibited by the sight of the apparatus, on another occasion responded violently to it. On this occasion it struck toward the bulbs at a distance of 52 cm. but when blindfolded it struck only at 25 cm. distance.

In all these experiments when the blindfolded snake struck at all it was invariably in the direction of the warm bulb regardless of its position at that moment in the apparatus.

The young boas struck more frequently at the warm bulb than did the adult snakes. Two protocols will illustrate.

Boa J₁, May 7, blindfolded, strikes at warm bulb 9 times in 5 minute period; distances 14, 14, 16, 16, 14, 18, 13, 13 and 17 cm. respectively. After the nostrils were plugged it struck 6 times in same period, distances 16, 17, 13, 12, 15 and 14 cm. respectively. After pits were closed no strikes were evoked.

Pits opened and 45 minutes later 7 strikes were made at warm bulb in 5 minutes, distances 18, 12, 16, 14, 11, 16 and 17 cm respectively. Tongue ablated and snake laid aside for healing.

May 11. Blindfolds replaced by new ones. Snake strikes 8 times at warm bulb in 5 minute period, distances 16, 14, 12, 18, 16, 11, 16 and 10 cm. respectively. Nostrils plugged with cotton and collodion, snake strikes at warm bulb 9 times in 5 minutes, distances 10, 16, 16, 15, 18, 12, 16, 20 and 11 cm. respectively

Boa J₃, May 7. Blindfolded snake strikes 7 times at warm bulb in 5 minute period, distances 16, 11, 14, 13, 18, 10 and 20 cm. respectively. Nostrils closed with collodion and cotton. Snake selects warm bulb 4 times in 5 minutes, distances 16, 12, 18 and 12 cm respectively. Pits closed with collodion, no strike could be induced during 45 minute period. Pits opened, 11 strikes directed at warm bulb in 5 minute period, distances 15, 15, 17, 14, 16, 12, 15, 15, 19, 14 and 17 cm respectively.

The young boas were more reactive and seemed to tire less quickly than did the adult boas. Extending the test period of adult boas did not always increase the number of strikes proportionately. One case will illustrate

Boa No 2, May 22. Blindfolded snake, tested during a 15 minute period, struck 10 times at the warm bulb, distances 24, 18, 18, 16, 15, 19, 20, 20, 18 and 19 cm. respectively. When its nostrils were plugged it struck only 5 times during a 15 minute period, distances 16, 17, 18, 16 and 16 cm respectively. With pits closed it failed to strike at all during the same length of time. When pits were freed again it struck 5 times during the same period, distances 16, 25, 20, 18 and 16 cm. respectively.

These reactions of *Boa hortulana*, both young and adult, to a warm, moving object are not found in boids devoid of labial pits. We have tested three Haitian boas, *Epiplatys striatus*, and two anacondas, *Eunectes murinus*, in the apparatus described above. None of the *E. striatus* struck at

either bulb when swung 10 or 15 cm. in front of the head. When the warm bulb was brought 3 or 4 centimeters away from the snout all three flickered their tongues vigorously toward it. When touched with the bulbs one of the three struck at both the warm and cold one. Blindfolding the three snakes prevented further striking at either bulb. A strong jet of air directed at the blindfolded snakes, caused them, however, to strike again in the direction of the irritation.

The two *E. murinus* available for this study differed from the *E. striatus* in their much more sensitive heads. They would respond almost immediately with a vigorous strike at either bulb when gently brought in contact with their heads. Other parts of the body were much less sensitive. Once a grip was obtained on the bulb several coils were thrown around it and the supporting apparatus. Since these anacondas were much larger than the boas they were much more difficult to handle. In spite of their more sensitive heads, they, like the Haitian boa, failed to distinguish between warm and cold bulb when swung a few centimeters in front of their heads.

Besides *B. hortulana* only one other boid with labial pits was available to us. This was the well-known green boa, *B. canina*. We have tested two adults of this species in our standard apparatus and found them to respond to the warm, moving bulb exactly as *B. hortulana* does.

The tendency of boids to flicker their tongues toward warm objects moved very slowly in front of the snout would indicate that the tongue may play a rôle in prey capture. *B. hortulana* was fed mice in our laboratory. In order to test the rôle of mouse odor in modifying the responses of this species to the moving bulbs, we killed a series of mice and hung each individual head down on either the warm or cold bulb. Although the presence of the dead mouse increased the tongue flickering it did not modify the response to the bulbs. The mice were chilled in order to prevent responses to their body temperature. When the bulb with the attached mouse was cold and motionless no strike occurred even when

a small fan was placed behind the bulb to drive the odor toward the snake. A record of further experimentation with one of the snakes may be given.

Boa 2, May 23 Blindfolded snake tested with mouse attached to warm bulb. A flickering of tongue but no strike made at this bulb while motionless. Air current produced by fan behind bulb causes flickering to continue but induces no strike. Bulb moved at 40 swings a minute induces five strikes in five minutes, distances 16, 17, 18, 16 and 16 cm. respectively, while fan is turned on. Snake strikes six times in five minutes at warm bulb with attached mouse when fan is turned off, distances 16, 18, 16, 16, 16 and 18 cm. respectively

This experiment was repeated with mouse blood and fur smeared on the rubber cover to the bulb. Only when this cover was on the heated bulb, and the latter was in motion, would the boa strike. The rapid flickering of the tongue toward the cover when motionless indicated that the snake was aware of the odorous substance which had been added to the apparatus.

EXPERIMENTS WITH CROTALID SNAKES

As stated in the first part of this report, the facial pit of the crotalid snakes differs remarkably from the labial pits of the Boidæ in that it is divided into two chambers by a membranous fold of skin. Series of *Agkistrodon mokasen*, *A. piscivorus*, *Crotalus adamanteus*, *C. horridus* and *C. viridis* have been available to us for experimentation. In our preliminary tests a marked difference between these species and the boids was noted. Crotalid snakes when blindfolded will strike at moving objects having no greater temperature than that of the surrounding environment. A cloth bundle, for example, tied to a stick and waved rapidly five or ten centimeters in front of both *Agkistrodon* and *Crotalus* will often induce a strike in the blindfolded snake. There is, however, great variability, many individuals not reacting at all. Vibrating the substratum either by thumping the cloth

ball against the floor of the platform or by agitating the platform with another stick would usually facilitate the reaction. If the eyes of the crotalid snakes were not covered, there was even greater variability, some snakes striking far more frequently and others not at all

When the crotalid snakes listed above were tested with the swinging bulbs and apparatus employed in the tests with boids other differences appeared. After every strike there was usually but not always a longer latent period before another strike could be induced. The crotalid snakes endeavored to escape from the apparatus more persistently. In order to secure uniform conditions of experimentation it was found necessary finally to disengage the paired bulbs from the moving arm and swing them by hand on the end of a long stick. This made it difficult to measure the striking distance with any accuracy. Hand manipulation did have the advantage that the cold bulb could be successively presented to the snake regardless of its position on the platform. If the snake consistently turned away from the cold bulb to strike at the warm it was further proof that the temperature difference was significant.

When allowance is made for this special method of handling the crotalid snakes and for their peculiarities of response a remarkable agreement is found between the reaction of the two groups of snakes to the swinging bulbs. One protocol for each of three species will illustrate.

C₁, June 15, adult *Agkistrodon piscivorus*, strikes at both bulbs when waved 10 cm. in front of head. When standard pads are adjusted over eyes the snake strikes only at warm bulb. Five strikes at this bulb in 2 minutes. Entire dorsal and lateral surfaces of head covered with collodion leaving only the pits free. When two bulbs are moved at approximately 15 cm. distance the snake strikes at warm bulb 3 times in 10 minutes.

June 16. All collodion removed from head of snake, eye pads readjusted and nostrils plugged with collodion and cotton. Snake now strikes 20 times in succession at warm

bulb although both bulbs held at same distance from head. Tongue removed completely Snake again offered both bulbs strikes at warm 24 times in succession and not once at cold. Greatest distance the bulbs elicited a strike was 35 cm. A ball of cotton on end of stick waved vigorously 10 cm. in front of snout, induces no strike A bottle of water heated to approximately 37° C. and moved in same manner as warm bulb induces four strikes in succession.

June 22 New eye covers and nostril plugs adjusted to this tongueless moccasin. When bulbs are moved at 32 cm. distance the snake strikes at warm one four times in succession Pits closed with collodion. No strike could be induced by moving bulbs at any distance from snout during 30 minute period. Pits are cleared of collodion and bulbs swung again in usual manner. Snake strikes at warm bulb twice in ten minutes

Cr₁, June 20, adult *Crotalus adamanteus*, strikes indiscriminately at either bulb swung close to face During ten minute period six strikes were at cold bulb and ten at warm Snake blindfolded now strikes only at warm bulb, ten strikes recorded in ten minutes Position of bulbs reversed at each strike. Eleventh strike at cold bulb. Next 17 strikes only at warm bulb in spite of its frequently changed relative position. Pits closed with collodion, no strike could be evoked by either bulb during one hour period.

June 21 Collodion removed from pits and a collodion patch 2 cm square attached to dorsal surface of head Snake tested again with bulbs strikes at warm one ten times in succession. The position of warm bulb relative to the cold one frequently changed. Nostrils plugged with collodion and cotton, tongue removed completely. Snake tested with bulbs strikes at warm one ten times in five minutes.

Co₂, May 4. Adult *Akistrodon mokesen*, tested before blindfolding, strikes at both bulbs moved before head. When paired bulbs are swung five to ten centimeters above snake's head, the snake turns and strikes 15 times at warm bulb and not once at cold. Eyes covered with standard pads, snake

strikes at warm bulb five times in five minutes. Cloth jackets to bulbs exchanged for new ones, and test repeated. Snake strikes at warm bulb six times in five minutes and not once at cold. Pits filled with collodion. No strike could be induced during thirty minute period. Collodion removed. Snake strikes three times at warm bulb during ten minute period

Our copperheads differed consistently from the other crotalid snakes in reacting quickly to a warm bulb swung above the head. In their ability to select the warm bulb they behaved like blindfolded crotalid snakes in our standard apparatus. The copperheads were also distinctive in striking at the warm bulb when touched with the cold one.

Although most of our experiments with crotalid snakes were carried out with adults we had one young cottonmouth, *A. piscivorus*, available. This individual responded very much like the adults. Part of the record for this individual will illustrate.

Ca, June 22. Young *A. piscivorus*, tested with bulbs after plugging nostrils and blindfolding, strikes only at warm bulb. Tongue removed and test repeated. Snake strikes twenty times at warm bulb and not once at cold although relative positions of bulbs frequently changed. Pits filled with collodion and test repeated. No strike in half hour.

June 23. Young *A. piscivorus* with nostrils plugged, eyes blindfolded, and tongue ablated, tested again after cleaning out facial pits. Snake strikes at warm bulb ten times in succession, the position of the bulbs relative to one another being frequently changed.

Although the above protocols might indicate that crotalid snakes are nearly as invariable as *Boa hortulana* in their response to warm moving objects, the record as a whole shows that a cold object moved vigorously may occasionally induce a crotalid snake to strike. A cold bulb moved in our test apparatus at fifty passes a minute induced a strike in some of our rattlers. Thus No. Cr₂, a diamond-back, nearly

six feet long a half hour after blindfolding struck twice at the cold bulb before directing any attention to the warm one. This snake after then striking four times at the warm, gave one more strike at the cold. The next six strikes were all at the warm. It might be assumed that such a record as this is due to a confusion of the snake perhaps induced by its strange environment. Later in the day this snake made no errors in eighteen strikes.

A series of tests made with blindfolded moccasins and timber rattlers reveals that these responses to cold moving object will occur more often in snakes having nostrils plugged and tongue removed than in those having their facial pits filled. In twelve different tests with *A. piscivorus* there were no strikes when the pit was filled, but six when nostrils were plugged, and tongue removed. One response occurred when the tongue only was removed, and one when the nostrils only were filled. In seven tests with blindfolded *Crotalus horridus* there were also no "errors" when the pits were filled but one when tongue was ablated and nostrils filled. These data substantiate the view expressed previously by Noble (1934) that the pits function in detecting air vibrations. It is obvious, however, from the above protocols that they have an even more important rôle in distinguishing warm moving objects from cold ones.

RESPONSES OF CROTALID SNAKES TO PREY

It has been shown above that both Crotalidæ and Boidæ provided with labial pits can distinguish temperature differences so slight that we have been unable to record them with sensitive mercury thermometers. The question remains, are they actually able to sense the body temperature of their prey while the latter is still at a distance? How great an increase in temperature is produced in the surrounding atmosphere by the warm body of active rodents on which these snakes feed? Employing the same combination of thermometers utilized in testing the air temperatures surrounding the bulbs, we found that a white rat raises the

temperature of the atmosphere 10 cm away approximately the same as our warm bulb raised the air temperature 20 cm distant. For example, an average reading when the room temperature was 25.2°C was atmosphere in contact with rat 32.2°C , 4 cm. away 25.65°C ., 8 cm. away 25.45°C , 10 cm. away 25.4°C . and 18 cm. away 25.3°C

Since our apparatus was obviously producing a heat gradient greater than could be expected of even the most active prey, we repeated our experiments substituting a freshly killed white rat for the warm bulb and a freshly killed but chilled rat for the cold bulb. These rats were the same size and were killed by a blow delivered in the same manner. Two adult *Akistrodon mokasen* were selected for testing. These had their eyes covered, nostrils plugged and tongue ablated before the rats were killed. On the first test one moccasin struck once at the warm rat, the other moccasin five times at it. Neither was attracted by the chilled rat. On a second test made with a second pair of rats prepared the same way the more reactive moccasin struck eighteen times at the warm rat but only once at the cold. The "error" was made at the moment when the two rats were in contact. Both snakes would strike at the cold rat when it struck their heads or when it was hit on the platform immediately before their snouts.

A third moccasin with eyes covered, nose plugged and tongue removed made an even better record with a third pair of rats. Before the warm rat grew cold it was struck at twenty-seven times. Two thrusts landed between the two rats. Only one strike was directed at the cold rat. It is therefore clear that the moccasins stripped of all their principal sensory mechanisms except their pits can still distinguish between freshly killed warm vs chilled rats.

HISTOLOGY OF THE PITS

The histological structure of the labial pits of boids has been described briefly by Lynn (*loc. cit.*) for *Boa canina* and in greater detail by Ros (*loc. cit.*) for *Python seba*. Neither

author described the nerve endings or even the distribution of nerve fibers in the epidermis of the pit. The structure of the facial pits of the Crotalidæ is much better known, thanks to the work of West (*loc. cit*) and especially Lynn (*loc. cit*). More recently one of us has pointed out that the nerve fibers in the pit do not terminate in sense cells as West and Lynn described but actually in knob-like enlargements which are widely distributed through the epidermal covering of the pit membrane (Noble, 1934). These endings are not associated with specialized sense cells and the elongated cells with "characteristic hyaline appearance" which Lynn describes appear to be cells which are undergoing the cytoplasmic changes which precede molting. Ros (*loc cit*) describes similar cells in *P. sebæ* and assumes that they assist the molting process. In our series of *B. hortulana* these cells are also abundant and associated with the molting process. Nerve terminations are no more numerous near these than near other epidermal cells.

The only feature which Ros found distinguished the integument lining the labial pits of Python from that of other parts of the head was the capillary net lying directly under the epidermis. In the pits of the upper jaw this net pushed partly into the epidermis. In *B. hortulana* the pits are well vascularized in the immediate vicinity of the nerves. Where nerve fibers penetrate the epidermis a small capillary may occasionally be found accompanying the fibers for a short distance. The nerve endings however lie distal to these capillaries and are not in contact with them. The epidermis lining the pits of the upper jaw is slightly thinner than that lining the pits of the lower jaw. Further, the nerves penetrate a more limited portion of the former. Hyaline "shedding cells" are present in the epidermis of all the pits and there is no enlargement of these cells in the pits of the lower jaw such as Ros (*loc. cit*) described in *P. sebæ*. In brief, the integument lining the labial pits of *B. hortulana* is essentially the same in the upper and lower labial shields. It differs from the integument covering the dorsal surface of

the head in its thinner epidermis, greater vascularity and far richer nerve supply

Ros (*loc. cit*) did not succeed in following the nerves supplying the pits to their endings. By using a modification of the Gros silver nitrate technique suggested by Dr G. F Laidlaw it has been possible to stain many of the fibers completely This technique consists in staining frozen sections with forty per cent silver nitrate after at least a month's fixation in pyridin-formalin. The sections are washed in twenty per cent and then five per cent neutral formalin After immersing in ammoniacal silver (ten per cent silver nitrate to which ammonia is added until the precipitate disappears) the sections are washed in five per cent hypo and mounted after clearing in xylol Such preparations vary considerably with slight changes in the periods of immersion in the different fluids. The preparations were supplemented by a series of pits fixed in Zenker's solution and stained with Mallory's triple connective tissue stain These were especially valuable in tracing the distribution of the capillaries

The pits in the upper labial shields of *B hortulana* are supplied by divisions of the superior maxillary branch of the trigeminal, those in the lower labial shields by the inferior maxillary branch of the same nerve Lynn (*loc cit*) has described and figured the distribution of the nerves in the closely related *B. canina* In *B hortulana* the conditions are essentially the same.

As shown in figures 1 and 2 the nerves after penetrating dermis break up into large numbers of unmyelinated fibers which extend for varying distances into the epidermis In sections 50 μ thick, individual fibers may be traced for distances of 111 μ in the epidermis The fibers end in knob-like enlargements which lie in contact with all of the different cell types found in the epidermis These endings have been found in both the germinative layer and in the flattened cells of the horny layer A photograph of some of the endings in the latter position is reproduced in figure 4. The greater number of endings are scattered throughout the various cells of the

intermediate layer of the epidermis. Epidermal cells lying adjacent to the endings do not differ in structure from surrounding cells in the same layer. Although it is often difficult to identify the cell walls in the silver preparations, a comparison with the slides stained with Mallory's connective tissue stain, clearly shows that even in the regions of the maximum abundance of nerve endings the epidermal cells remain unspecialized

In some of the silver preparations (Fig 2) the course of the capillaries may be followed. The nerve fibers after leaving their connective tissue sheaths frequently twist around the capillaries lying in the superficial layers of the dermis. In this way a rich blood supply to the fibers is assured. Frequently a fiber will branch at the point of contact with a capillary and the separate divisions will extend up either side of the capillary to penetrate the overlying epidermis (Fig 1). It would seem as if the distribution of the capillaries was partly responsible for the brush-like form the nerves assume after breaking free from their connective tissue sheaths

The histological structure of the facial pit of the crotalid snakes has been described by West (*loc cit*) and by Lynn (*loc cit*). As stated above the membrane which is stretched across the bottom of the pit is known to have a very extensive innervation from the ophthalmic and supramaxillary branches of the fifth cranial nerve. The facial pit arises from two invaginations (Fig 5) which, on growing deeper, thin out the wall between them to form the membrane. The caudal pit begins to form after the cranial one is clearly marked out. It remains smaller than the cranial one and its epidermis which covers the rear wall of the pit membrane has fewer cell layers and a thinner horny layer or cuticle than that of the cephalad pit. The epidermis of the latter eventually forms the anterior surface of the pit membrane. A series of drawings of embryos studied by Dr Manning shows how the pit membrane forms. One drawing of this series is reproduced in figure 5.

In the adult snake the much thinned wall between the two

pits of each side is reduced to the two sheets of epidermis separated by a thin layer of white fibrous connective tissue. This middle layer forms the bed for the numerous nerve bundles which invade it from all sides. It further agrees with the dermis of the labial pits of boids in its rich capillary supply. Figure 7 shows a tracing of the capillaries which Dr Manning found in one square millimeter of pit membrane in the diamond-back rattlesnake. A further agreement between crotalid and boid pits is that the nerves on entering the dermal tissue follow the blood vessels for a short distance. The larger bundles fan out into numerous nerve fibers which spread until they overlap the fibers from adjacent bundles.

In the pit membrane of the very young crotalid the median layer of connective tissue is thick and cellular (Fig 9). In the adult the membrane has become very thin and the nerve fibers make up the bulk of the median layer. The inner epidermis is extremely reduced and closely applied to the nerve bundles (Fig 8). Numerous nerve fibers extend outward from these bundles and form a dense ramifying net between the cells of the outer epidermis of the membrane. The knob-like nerve endings are numerous in this outer epidermis but in cross-sections of the pit membrane they often resemble twisted fibers cut at oblique angles. The nerve endings are in contact with the several cell types found in the outer epidermis. They have been identified in methylene blue, Cajal 3A, Boule B and modified Gros preparations. Like the conditions in boids, the epidermal cells with which these endings make contact are not specialized. The clearer cells which both West (*loc. cit*) and Lynn (*loc. cit*) described as sensory cells may or may not have nerve terminals in contact with them.

The pit membrane of crotalid snakes shows in histological detail a close resemblance to the labial pits of boids. If two pits in the upper jaw of *B. hortulana* could be pressed together during ontogeny until merely a membrane remained between them, a structure would be formed very similar to the facial pits of crotalid snakes. As a matter of fact the ontogenetic

changes mentioned above actually indicate such a duplex origin of the crotalid facial pit. Further adjustment would consist merely in a reduction in size and functional importance of the caudal pit. This would presumably go hand in hand with a reduction of its innervation. In the adult crotalid there is no evidence that the inner epidermis of the pit membrane, that is the anterior wall of the old rear pit, is actually innervated. It is reduced to such a thin covering over the nerve fibers that there is little room left for the nerve terminals.

DISCUSSION

We have been able to confirm Ros (*loc cit*) that a motionless source of heat placed in front of a boid calls forth a reaction, frequently an approach. But colubrids entirely devoid of pits will also approach a heated area. We found that *B. hortulana* blindfolded and deprived of labial pits was stimulated by such a source of heat, at least when this was directly in front of the snout. It seems that in both boid and colubrid the sense organs in the general integument of head or body may serve in temperature discrimination. Some preliminary observations on *Thamnophis sirtalis* have indicated that its ventral surface is more sensitive to temperature change than is its dorsal surface. In *B. hortulana* our observations reported above indicate that the snout is more sensitive than the side of the head.

Ros (*loc cit.*) made no attempt to determine the function of the pits of boids in detecting warm objects in motion. This it appears from our experiments reported above is the chief function of the pits. Boids provided with pits strike at warm moving objects with remarkable regularity and their ability to discriminate between extremely small temperature differences is apparently excelled in the vertebrate series only by fish.¹

Although various investigators have compared the labial pits of boids with the facial pits of crotalid snakes no one has previously shown that they have identical functions. The

¹ See recent paper by Bull, H O, 1936, Jour. Marine Biol Assoc, 21, 1-27

structural differences between these two sets of structures have appeared very great to these previous workers. There are, however, many similarities, especially in the knob-like nerve endings scattered between the cells of the epidermis and unassociated with any specialized "sensory cells"

Recently it has been shown that the lateral line organs of fish aid in temperature discrimination (Hoagland, 1935) although they also have other functions. Lateral line organs are not found in terrestrial vertebrates and were presumably entirely absent in the saurian ancestors of the snakes. It is interesting that when a new organ of special temperature sense was developed in the Serpentes that not a lateral line nerve such as the seventh or ninth cranial but a new nerve, the fifth, should have specialized for this purpose. Further, different areas of the integument were modified in crotalids and boids. It is possible that still a third area was modified in certain viperids. At least a pit has been described from the dorsal surface of the snout in several species of *Bitis* (Parker 1932). In this connection it is interesting to note that some species of the group strike upwards and even caudally over their backs, a feat unknown in the crotalids supplied with pits on the side of their heads.

The most highly developed pit is found in the crotalids and here it appears to have functions in localizing the direction of air vibrations as well as in detecting warm blooded prey. These crotalids when blindfolded and stripped of olfactory and Jacobson's organ sense will still strike at cold moving objects which fail to arouse them after their facial pits are eliminated. The more primitive boids deprived of the same distance receptors fail to strike under identical conditions. The drum membrane of the facial pits is an ideal mechanism for receiving air vibrations. Both ontogenetic and anatomical evidence indicates that the facial pit was evolved by the fusion of two pits of the type found in boids. This primitive mechanism was a thermal receptor and not an air movement detector. But even in the most advanced crotalids the response to a warm moving object predominates. There is

no evidence that the assumption of this new function of recording air vibrations in any way impaired its original function as a thermal receptor

It is perhaps fortunate for man's safety that crotalid snakes are far less mechanical in their response to warm objects than are the harmless boids. This is partly due to the greater importance of visual impulses in modifying the responses in this group, and partly to their more rapid "taming." Copperheads, timber rattlers and moccasins which had been frequently handled before coming to us failed entirely to respond to our test objects. The natural history literature has frequent reference to the rapid "taming" of crotalid snakes (as for example Wiley, 1930). It is well known that various crotalids may feed on cold blooded prey. In these cases visual impressions rather than facial pit stimulations must have controlled the behavior.

In order to evaluate better the importance of vision in the feeding of rattlesnakes we have tested a series of *Crotalus viridis*. Ten days after removing the tongue and four days after eliminating the pits completely by cauterization one snake ate two mice within a period of forty-eight hours. Another pitless and tongueless rattler devoured one mouse in the same period. Rattlesnakes therefore deprived of their pits and tongue are perfectly capable of catching and devouring prey unaided. Noble and Clausen (*loc cit*) have showed that in some colubrid snakes olfaction alone was adequate for food seeking and feeding. It appears then that although crotalid snakes are highly specialized in the extreme elaboration of the tongue-Jacobson's organ mechanism for trail finding and the facial pits for warm blooded prey detection, the primitive olfactory and visual mechanisms still have important functions. Further they may suffice alone under ideal conditions of food capture such as maintains in a large laboratory cage. Crotalids deprived of pits and tongue would doubtlessly have a difficult time under natural conditions for both structures have important sensory functions.

CONCLUSIONS

1. Boid snakes provided with labial pits (*Boa hortulana*, *B. canina*) can discriminate perfectly between temperature differences of 0.2°C and considerably less. When blindfolded they can distinguish between warm and cold covered electric light bulbs moved together on a mechanical arm.

2. Blindfolded crotalid snakes can also distinguish between very slight temperature differences in moving objects, but they will also strike at cold objects moved vigorously before them.

3. Elimination of the principal sensory mechanisms of the head has shown that the labial pits of boids and the facial pits of crotalids are the thermal receptors which function in this fine discrimination.

4. These snakes are able to detect their prey by sensing their body temperature at a distance.

5. Both labial and facial pits are innervated by the fifth cranial nerve and in both the nerve terminations are knob-like enlargements lying between the unspecialized cells of the epidermis.

6. The ontogeny indicates that the facial pit of crotalids was evolved by the partial fusion of two pits of the type found on the lips of boids. The intervening wall between the pits remains as a drum head, the facial pit membrane.

7. Although this phylogenetically more recent structure, the pit membrane of crotalids has assumed the new function of detecting air movements, it has not lost its more primitive function of temperature discrimination.

8. In the absence of vision, crotalids respond more consistently to the warmth of a moving prey's body than to the movements alone.

9. Both in boids provided with labial pits and in the pit vipers the odor of the prey evokes tongue movements while the temperature gradient from the prey's body calls forth the strike.

10. In the absence of vision the labial pits of Boidæ and the facial pits of Crotalidæ are the most important sensory

mechanisms for directing the strike towards warm blooded prey

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PLATE I



FIG 1 Section vertical to surface of labial pit of *Boa canina*, stained by modification of the Gros silver nitrate method *f*, Blood vessels *B*, Intraepidermal nerve fiber $\times 168$

FIG 2 Similar section of labial pit of *Boa hortulana*, stained by same method as Fig 1 *A*, Capillaries lying directly under epidermis *B*, Nerve bundles supplying labial pit $\times 168$

PLATE II



FIG. 3. Section vertical to surface of epidermis lining labial pit of *Boa hortulana*, stained by same method as Fig. 1. *A*, "Shedding" cell. *B*, Nerve fibers penetrating epidermis. *C*, Intraepidermal nerve fiber cut in cross section. $\times 860$.

FIG. 4. Another portion of same section as Fig. 3, showing more of the dermis. *A*, Nerve ending in epidermis. *B*, Nerve fiber below epidermis. $\times 860$.

PLATE III

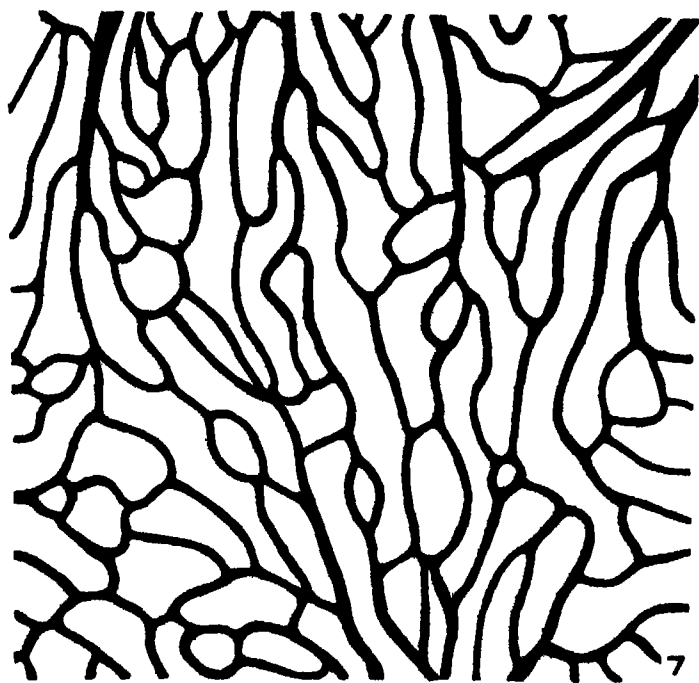
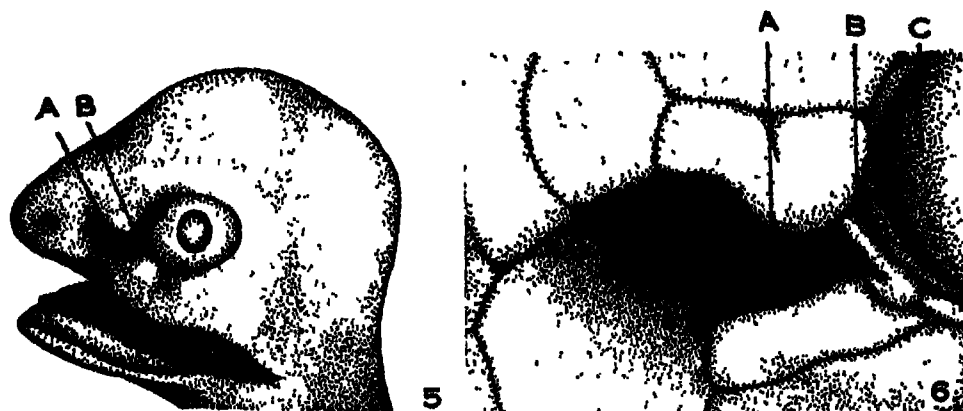


FIG. 5 Head of embryo of *Agkistrodon mokasen*. Original study by Dr. F. B. Manning. The caudal pit (B) beginning to form within margin of main pit (A). $\times 76$

FIG. 6 Facial pit of adult *Agkistrodon mokasen*. Original study by Dr. F. B. Manning. The caudal pit now opens by a pore (B) anterior to the eye (C). The main pit (A) is relatively nearer the eye than in the embryo. $\times 32$

FIG. 7. Camera drawing of 1 sq mm of facial pit membrane showing distribution of the capillaries. Original study by Dr. F. B. Manning

PLATE IV



FIG 8 Section vertical to surface of pit membrane of the facial pit of *Crotalus horridus* stained by Cajal 3A method A, Cuticle of main pit B, Epidermis of main pit with branching nerve fibers C, Nerve fibers below epidermis of main pit D, Epidermis of caudal pit E, Capillary $\times 570$

FIG 9 Section vertical to the surface of pit membrane of *Agkistrodon piscivorus* embryo stained with hæmatoxylin-fuchsin A, Cuticle of main pit B, Epidermis of main pit C, Nerve trunks below epidermis D, Epidermis of caudal pit $\times 515$

PLATE V

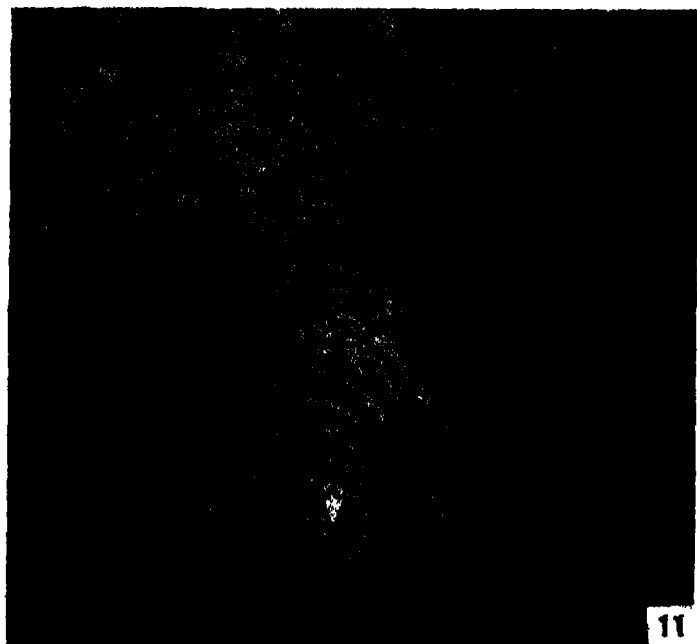


FIG. 10 Section vertical to the surface of pit membrane of *Crotalus horridus* in region of large nerve bundle, stained by Cajal 3A method A, Cuticle of main pit B, Epidermis of caudal pit C, Nerve fibers penetrating epidermis of main pit D, Nerve trunk below epidermis of main pit $\times 513$

FIG. 11 Whole mount of pit membrane of *Crotalus adamanteus* viewed from inner surface, stained by pyridin silver nitrate method A, Nerve ending $\times 860$

CENOZOIC CYCLES IN ASIA AND THEIR BEARING ON HUMAN PREHISTORY

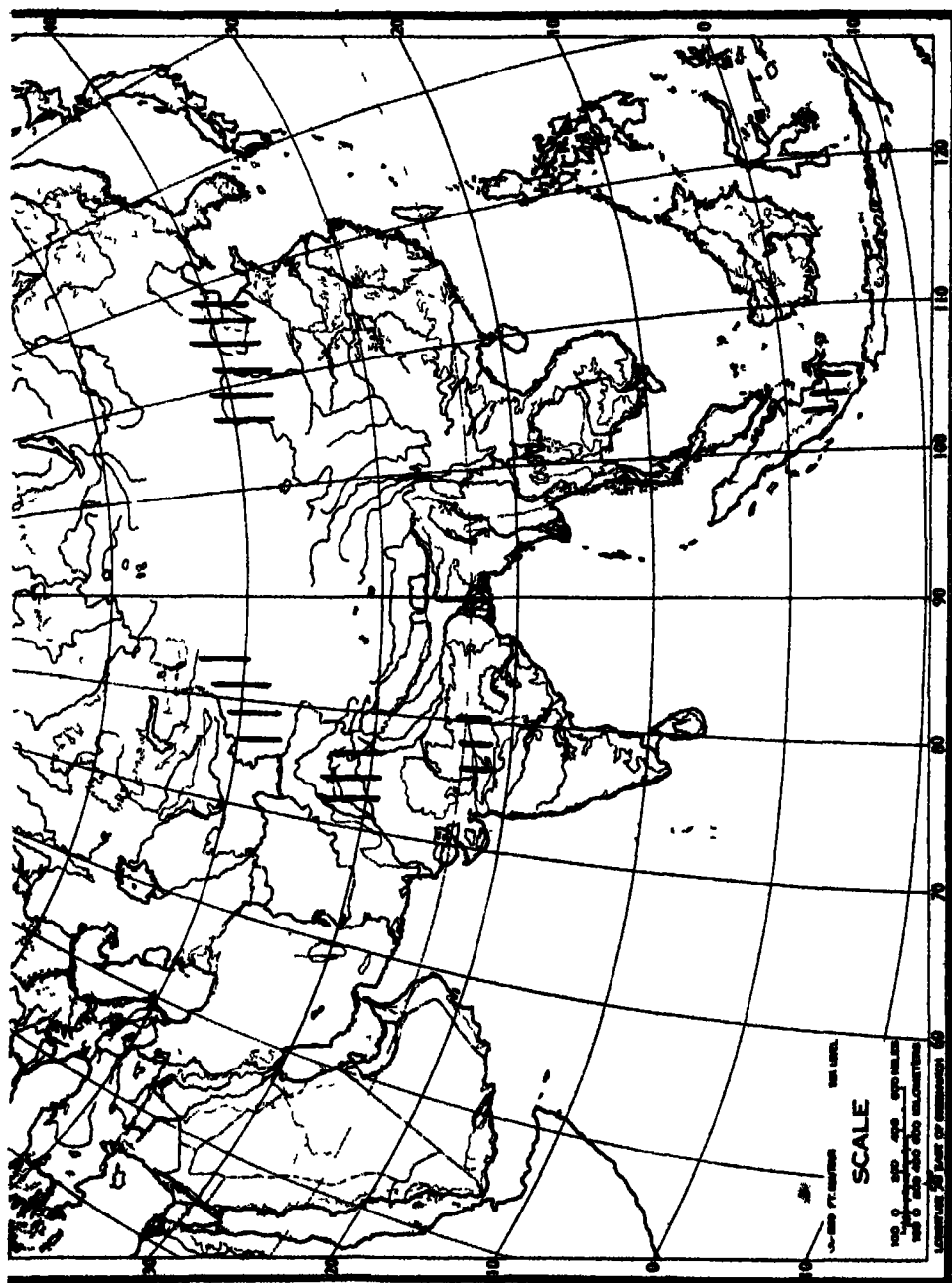
HELLMUT DETERRA

(Read November 27, 1936)

ABSTRACT

An attempt is made to apply the cycle theory, as worked out by the investigators of Fossil Man in China, to other regions in Asia, especially India and Java, from where new geologic and archeologic data have recently been recorded. It was found that on geologic, paleontologic and archeologic grounds correlations exist between certain Pleistocene stages and distribution of prehistoric cultures. One of these reveals the appearance of Old Paleolithic industries in the Middle Pleistocene, specifically at the close of the second glaciation and during the following interglacial (or interpluvial) interval. Another important stage in the evolution of Man is marked by the occurrence of anthropoids in the Pliocene of India in which group a progressive tendency of specialization is apparent. These facts suggest that the late Pliocene cycles witnessed the critical phase in the evolution of Man in Asia, as also that Man existed in widely scattered regions as a migrating hunter during the Middle Pleistocene.

THAT human prehistory in Asia is intimately linked with the geologic fate of this continent has been demonstrated in China by various investigators. In the geochronologic calendar as worked out by Teilhard, Barbour and Young (1933), the 'red letter days' of early human existence appear within distinct geologic cycles or time units. Peking Man, for instance, lived at the time of cycle 4, in which the Choukoutien cave formation represents the Middle Pleistocene. A younger Mousterian type of culture, found at the base of the famous loess, belongs to cycle 5 of the Cenozoic history of China. The appearance of man at a given time period within a sequence of five geologic cycles makes one speculate as to their meaning in relation to human prehistory in Asia. It arouses one's curiosity to see whether the 'red letter days' on the Chinese geologic calendar hold good, also, for other regions, such as India and Java from where Paleolithic cultures and fossils have lately been reported. The geologic synchronization of culture-bearing strata over such wide distances



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FIG. 1 Map showing regional distributions of areas under discussion

would indeed involve liberal speculation were it not for the fact that with new data on hand from India it is possible to correlate certain sequences by means of fossil, cultural and geologic records

At first it is necessary to review briefly what the cycle theory of the investigators of Peking Man represents and then an attempt will be made to compare their analysis with the records found in India and Java

CHINA

In the Hoangho basin and adjoining regions of north China five stratigraphic cycles are represented, each of which is typified 'by the same succession of sedimentary phases (basal gravel—sand—loam or loess), by the same group of corresponding facies, by special terraces, and by a characteristic fauna' (1933, p 51), Fig 2

		Formations	Cultural and fossil record
PLEISTOCENE	Cycle V erosion	Djalai Nor deposits	Mesolithic Djalai Nor culture
		<i>Malan loess-Sjara-osso-gol basal gravel</i>	Mousterio-Aurignacian of Ordos and adjoining regions
	Cycle IV erosion	red loam, gravel terrace	Old Paleolithic industry of Choukoutien <i>Sinanthropus pekinensis</i>
		<i>Choukoutien cave deposits</i> Siphneus tingi beds	
PLIOCENE	Cycle III erosion	<i>Sanmen formation red loams</i> Nihowan and Shansi Equus beds	
	Cycle II erosion	Gravel terraces along Hoangho red loam	
	Cycle I	<i>Paote formation</i> Hipparion richthofeni beds	

FIG. 2 Cenozoic sequence in North China

The cycles range from the lower Pliocene to the upper Pleistocene. The first cycle, or Paote formation, is lower

Pliocene (Pontian). Its strata rest disconformably on the peneplain surface of older rocks. The remains of the three-toed horse (*Hipparion*) and of the rodent genus *Prosiphneus* are here embedded in red clays in association with warmth-loving forms (*Giraffida*, *Antelopinae*, *Mastodon* and others).

The second cycle, for want of a better name, signified by the letter "Y," represents the middle Pliocene and is separated from the preceding cycle by a period of erosion. At that time the fauna still resembled the Pontian but certain *Antelopinae* and a new species of *Prosiphneus* approach already certain modern Asiatic types (*Procapra* and *Siphneus*). The prolific variety of hoofed animals in this fauna suggest perhaps open grazing grounds and a climate of somewhat drier type.

In the following cycle 3, the fauna is thought to be of late Pliocene (Villafranchian) age, that is so far as the Nihowan beds are concerned, yet the appearance of true horse heralds the arrival of migrating forms generally recognized as Pleistocene types.

In 1933 the authors of "Fossil Man in China" included the *Siphneus tingi* beds (Red concretinary loam) in this late Pliocene stage but Teilhard and Young (1935, p. 174) have recently assigned these to the lowest Pleistocene which would bring them into the following cycle 4. Since these beds overlie unconformably the late Pliocene rocks it is evident that cycle 3 ends with the Pliocene and that the Pleistocene cycle 4 begins with erosion and subsequent deposition of red loam.

The early Pleistocene or cycle 4 embraces both lower and middle Pleistocene and in it Peking Man appears in the Choukoutien formation. This middle Pleistocene stage of Choukoutien terminates cycle 4. At that time a coarse river deposit was formed which the excavators have tentatively correlated with the late Mindel or second glaciation in Europe. Its fossils, however, are thought to indicate a mild climate for which the red staining of the loams may in part be held responsible. The fauna of Peking Man includes two forms, namely, *Elephas cf. namadicus* and the wild boar, *Sus*

lydekkeri, which also appear as guide fossils in the middle Pleistocene of India.

As to the culture of Peking Man, represented by the industry of Choukoutien, Weidenreich (1936, p. 47) has recently again emphasized the 400 ccm brain superiority of *Sinanthropus* over the apes. This, he thinks, permits of recognizing Peking Man as manufacturer of stone tools. The Choukoutien culture is characterized by the absence of bifaces and by an autochthonous emergence of a core-flake industry of very primitive origin. Hence it is for the present to be considered as an 'atypical' industry in regard to its typologic relations with European standards.

Finally cycle 5 is represented by the great loess formation of China which the previously named investigators were inclined broadly to correlate with the last glaciation of Europe. This would mean that the preceding period of erosion, which Barbour (1926) has called Chingshui, covered two interglacial and one glacial stage. This is a very long interval considering that, typologically spoken, the Middle Paleolithic industry below the loess does not seem so very far removed from the culture of Peking Man. This may mean that the early Paleolithic has here, as in Europe, a very long stratigraphic range. The loess itself contains Paleolithic workshops of the Mousterian-Aurignacian type (Boule, 1928). The Mongolian sands which contain *Rhinoceros*, *Bos* and *Elaphus*, carry an Upper Paleolithic (partly microlithic) culture in which deer antlers were probably utilized for tools. In Mongolia the preceding cycle 4 is obscure but cycle 3 is represented by consolidated piedmont gravels and sandstones which cover the 'Gobi erosional plane' of Berkey and Morris. To cycles 2 and 1 belong here the Ertemte sands and White Beds of Dalai Nor and the red earth of pre-Sanmenian age as also the fossiliferous Pliocene beds of the Kalgan and Dalai Nor regions (1933, p. 56). From the Ertemte sands of Mongolia Schlosser (1924) described a single molar of a new species of *Pliopithecus*. This is the only anthropoid fossil found so far in northern China.

In Central Asia, the cycles were recorded in a somewhat different fashion because of the young mountain making movements to which the Tienshan and K'un-lun ranges were subjected (Fig. 3). In their foothills the late Pliocene gravel

PLEISTOCENE	Cycle V	loessic loam and gravel		
		main loess basal gravel		
	erosion			
	Cycle IV	gravely sand, little consolidated		
	erosion	conglomerate and sand		
		sandstone and clay, pink-grey	Bora series + 2000 ft	Folded ----->
PLIOCENE		siltstone and clay		
		sombre colored conglomerate		
	erosion			
	Cycle III	conglomerate (variegated)		
		clay and sandstone		
	?	sandstone, silt (greenish-grey) *	Kokyar-series + 4500 ft	
		silt and sandstone (red) basal conglomerate (red)		

FIG. 3 Siwalik sequence in foothills of Western K'un-lun (Sinkiang)

fans are folded and between them and the loess a set of two terraces was observed near Turfan which presumably represent the intermediate fourth cycle (1933, p. 58). From southern Sinkiang, south of Yarkand, I have described a loess sheet which covers tilted terrace gravels, sands and silts to which I gave the name Bora-series (1932, p. 63ff). These beds resemble the Upper Siwaliks of northern India both as regards their lithologic composition and their unconformable contact with the underlying Tertiary red beds or 'Kokyar series.' This unconformity doubtless signifies the same period of erosion which is uniformly recorded above the Pliocene formations in China and India (Figs. 2, 4). The Old Pleistocene or 'Bora-series' exhibit here a disconformity between a

lower pink or brown colored silt-sand and a lighter conglomerate-sand complex, thus indicating a revival of fan deposition at the close of cycle 4. Hence it seems that the normal sedimentary cycle (gravel—sand—loam) under 'Siwalik conditions' is broken up into two sub-cycles of which the younger reveals a phase of intensive uplift with resulting fan deposition. The absence of detailed stratigraphic data on the Tertiary red-beds of the K'un-lun foothills does not as yet permit recognition of the earlier Cenozoic cycles.

To sum up in China the oldest human culture appears in middle Pleistocene river deposits belonging to cycle 4. The middle and upper Paleolithic is connected with the loess cycle 5. No good records of anthropoids are known from either Central Asia or North China and although the 'Siwalik condition' is found on the borders of the Tarim basin there is here no indication of a rich fossil fauna such as characterizes the Siwaliks of northern India.

INDIA

In contrast to the incompletely known record of the Cenozoic in Central Asia, both as to fossil and cultural remains, India presents a much more complete picture. This is due mainly to the greater accessibility of the region for students of geology but also due to the fossil wealth of the Cenozoic formations, to the clear documentation of both orogenic phases and Ice Age cycles, and to the presence of such prehistoric cultures as permit of typologic correlations (Fig. 4).

The Cenozoic history is here mainly recorded by the Siwaliks, a formation of freshwater deposits more than 20,000 feet in thickness, which ranges in age from the late Miocene to the Middle Pleistocene. So far as the lower and middle Siwaliks are concerned no stratigraphic breaks are discernible which might help to distinguish definite cycles, as in China. Colbert (1935) regards the Chinji beds in the lower Siwaliks as Pontian which in China embraces cycle 1, but in India there is apparently no break between the Pliocene and the Miocene and hence it remains doubtful from the outset

Formations in Punjab			Glacial cycle in Kashmir	Cultural and fossil record	
PLEISTOCENE	warped	upper	redeposited silt and loam	4th Glaciation terrace IV	Mesolithic
			erosion	3rd Interglacial terrace III	Soan cultures Chelleo-Acheulean
			Potwar loessic silt and basal gravel	3rd Glaciation terrace II	
	middle		long period of erosion highest gravel terrace on Soan river	2nd Interglacial terrace I Upper Karewas	
		folded	Upper Siwaliks	Boulder Con- glomerate and silt	2nd Glaciation Karewa gravel
	Pinjaur zone			1st Interglacial Lower Karewas	
	Tatrot zone conglomerate			1st Glacial lowest moraines and fan deposits	
PLIOCENE	lower	Middle and lower Siwaliks	Dhok Pathan zone	progressive anthropoids	
			Nagri zone		
			Chinji zone		

FIG. 4. Cenozoic cycles in NW-India.

whether the cycle theory is applicable to this region. A significant break, however, divides the Middle from the Upper Siwaliks, and in it one can recognize, as Dr Teilhard and myself (1936) have recently shown, the boundary between the Pliocene and Pleistocene periods. It signifies a period of erosion (initiated by uplift of the Himalaya) as well as change of fauna. The late Pliocene Dhok Pathan stage contains anthropoids, the lower Pleistocene Upper Siwaliks has so far yielded none of these forms except for a canine of *Sinia* of doubtful origin.

In view of the fact that the basal Upper Siwaliks are in

parts correlatable with the first mountain glaciation in the Himalayas, the unconformity with the Middle Siwaliks must also signify a climatic change which, somehow, should have been connected with the geographic changes introduced during the late Pliocene by the Himalayan mountain uplift. These climatic changes deserve closer attention in connection with the problem of anthropoid evolution in the Himalayan region and it is therefore of interest to discuss briefly the geological factors which must have influenced the evolution of the higher anthropoids in the Siwalik region. These were principally of two kinds. On the one hand they were determined by a temporary stability of crustal and atmospheric conditions during the greater part of the Pliocene period, and on the other by climatic changes and paroxysmal manifestations of mountain uplift towards the close of the Pliocene and during the Pleistocene.

At the beginning of the Pliocene, that is to say during the Chinji stage, the Himalayan foothills presented an open country of low relief. This is borne out by the fine grained nature of the fluviatile sediments which indicate continuous but rapid accumulation in wide flood plains. Quick lateral changes of facies reveal constant shifting of wide stream channels such as characterize some of the larger Himalayan rivers in the northern plains of present-day India. These ancestral rivers must have been well graded as the sandy components in the Siwalik beds gradually increase towards the mountainous tract. The relief of the adjoining mountains therefore was mature and obviously much lower than at present. Complete remnants of this old landscape have been preserved in Tibet but the Himalayas as a whole bear unmistakable signs of this flat relief (deTerra, 1934, 1935). This naturally made for an evenly inclined mountain slope, favorable for a relatively uniform vegetation.

Little has been preserved of this vegetation in the Lower and Middle Siwalik beds but fragments of palms, leaves, and a few thin layers of lignite. The latter, if properly studied for their possible pollen content, might throw new light on the

climate and flora of Siwalik time. Until this has been done a paleoclimatic analysis must rest on the lithology and fauna.

The Chinji beds are mainly composed of red silt and clay, alternating with red and grey sandstones. The dark red color, so typical of this stage, would indicate an abundant supply of solvent agencies leading to hydration of ferromagnesian minerals under the influence of weathering and erosion in the ancestral upland. From there the red colored weathering products were swept into the lowlands where they accumulated. Laterite soils might have been a source for the red color which partly may also have been derived from exposure of older formations, such as the Murree and Kamliyal beds (Miocene) which are both of red or purple color. Solvent processes, such as these, require abundant rain fall and vegetation and become most effective if the precipitation occurs intermittently so that red soils can form. That rain falls changed with drier seasons during Siwalik time is also indicated by the appearance of certain wash-products, called 'pseudo-conglomerates' by Indian geologists. They consist of firmly cemented limonitized pellets which doubtless originated from silty soils undergoing repeated soaking and drying. These weathering products were finally swept together by rain and river action which explains why they are so rich in fossil teeth and bones. The latter are hardly ever rolled and show no signs of silicification, but are more often embedded in a red clay matrix.

The younger Nagri zone is mainly made of pepper colored and grey-greenish sandstone with red clays intercalated. In some of the sandstones feldspar and dark minerals are preserved which might indicate that chemical weathering was less active during this stage than in the previous period. However, palm leaves are locally abundant so that the climate of Nagri time must have been at least sub-tropical if not tropical. The sparseness of fossil leaves suggests that the forests were rather localized as in savannah countries of southern latitudes. This view is also supported by the abundance of ruminants and grazing animals, as recorded by the Middle Siwalik fauna.

More arid conditions however may have prevailed during Dhok Pathan or later Pliocene time. This stage is made of thick feldspathic sandstones of grey and whitish color, interbedded with orange and red clays. Chemical weathering, evidently was less effective during this period the deposits of which resemble somewhat the sediments laid down in the semi-arid, monsoon swept plains of Northwest India.

As the sedimentary records suggest a gradual change from tropical to more arid conditions so do certain faunistic elements. Fossil remains of anthropoids of which 8 genera and 21 species have so far been distinguished (Colbert, 1935, pp 29-30) are more abundant in the Chinji and Nagri zones than in the Dhok Pathan. In the earliest Pleistocene (Tatrot beds) they are entirely absent. This fact is very suggestive for the existence of a tropical climate during the pre-Dhok Pathan stages of the Siwaliks. Interesting also is the association of anthropoids with *Giraffokeryx*, an okapi-like animal the descendants of which still live in tropical Africa where anthropoids are known. The Pliocene horse *Hipparion*, on the other hand, being a grazing animal of the open plains, becomes most abundant in the Dhok Pathan zone while only few remains have been recorded from the Chinji beds. This may not so much be due to the late arrival of the horse in India, as to the tropical nature of the country which gradually offered large grazing grounds as the climate became more arid. The same explanation is offered for the wealth of large giraffes, antelopes and bovids which characterizes the Dhok Pathan fauna. It is as if the country along the Himalayas had become more open and drier as the Upper Pliocene began. In respect to anthropoids it is highly significant that their fossil remains are most common in regions which were upland, such as at Haritalyangar and Chinji, on the slopes of the Himalaya and Salt Range respectively. These elevated regions doubtless were then jungle clad, in a similar way as the present Himalayan slopes in Assam and Burma are where the gibbon still inhabits the mountainous monsoon-swept forest.

From these data it would appear that the Chinji and Nagri

zones offered the most favorable habitat for anthropoid evolution which is the lower and presumably the middle Pliocene. This time still comprises a unit of several million years, a period sufficiently long for the gradual emergence of proto-human types.

The great gap in our records between the anthropoid bearing beds and the implement bearing Pleistocene formation coincides with a period of great geologic unrest. This is documented by (1) the sudden coarseness of deposits in late Dhok Pathan time, clearly indicating rejuvenation of drainage in the Himalayan upland, and (2) by the disconformable, often unconformable, nature of the Pliocene-Pleistocene boundary (deTerra and Teilhard, 1936). Both features point to a paroxysm of Himalayan mountain uplift which—and this should be noticed—lags somewhat behind, what one might call, a period of accelerated anthropoid evolution. If the emergence of proto-human forms had anything to do with this critical phase, as Pilgrim (1915), Grabau (1935) and Black (1924) anticipated, it is obvious that this event may be looked for in the Dhok Pathan and Nagri zones of Siwalik time when stress conditions, due to climatic changes, should have promoted the evolution of progressive types¹. So far as this event can be supported by anatomical evidence it appears that the Himalayan uplift was only loosely connected with it, in fact it would seem as if the climatic changes known to have occurred in the Pliocene of Europe, from warm-humid to cold-arid, had equally, if not entirely, influenced early human origins in India. Taking into consideration the faunal character of the Upper Pliocene in India and China one might well say that the Dhok Pathan beds represent cycle 3 and that the emergence of proto-human forms might accordingly be expected in either the 3d or 2d cycle. This contention is in support of Pilgrim's (1915, p. 3) view regarding the pliocene origin of man in India.

¹ The new age interpretation of the Siwalik stages initiated by W. D. Mathew (1929) and further developed by Colbert (1935), deTerra and P. Teilhard de Chardin (1936) demands a new orientation of speculations regarding the age of the critical evolution in the Siwalik anthropoid group.

What makes the Siwalik history more interesting than ever is the discovery of prehistoric tools in the topmost gravels of the Upper Siwalik formation as recorded by the author and T. T. Paterson (1936). Where the early Pleistocene (Tatrot-Pinjaur) beds are missing the implement bearing gravels of the Boulder Conglomerate stage rest unconformably on the Dhok Pathan beds which contain anthropoid fossils (Fig. 5). In such a case the hiatus conceals in rather dramatic fashion the hypothetical period of human emergence.

The interval represents a long time period recorded by the bulk of the Upper Siwaliks. These we can divide into two faunistic and lithologic sequences or subcycles which are of early and of middle Pleistocene age. The former is characterized by an antique Pleistocene mammal fauna in which primitive elephants, also *Stegodon*, *Hemibos*, *Equus* and *Sivatherium* figure prominently. In it sedimentation proceeded from coarse gravels to silt and loamy deposits. The second subcycle or Boulder Conglomerate zone can definitely be correlated with the second Himalayan glaciation (? Mindel in Europe). It attains enormous thickness and everywhere it is either warped or folded (Fig. 6). The few fossils known seem to indicate a younger type of fauna in which the Indian variation of *Elephas antiquus*, (*Elephas namadicus*) appears.

In the topmost gravels, belonging either to this horizon or to a slightly later stage the first true prehistoric tools appear. They are crude split pebbles and large flakes of quartzite chipped on one side mainly with large bulbs of percussion, small striking platforms and marginal flake-scars (Fig. 7)¹. It is a pre-Chellean complex whose age we can assign to a retreat phase of the second glaciation which may have lasted into the beginning of the second interglacial. This second interglacial saw the emergence of Old Paleolithic cultures which are recorded in two major facies, a Chelleo-Acheulean

¹These photographic reproductions of artifacts were made in the field which accounts for their incompleteness. At the time of writing they were the only ones available to the author who sent his Paleoliths to Cambridge, England for study. Preparation of two volumes dealing with the geology and prehistory of Early Man in India is under way.

hand-axe and an 'atypical' complex of pebble- and flake-tools which I have provisionally named Soan culture. The Chelleo-Acheulean hand-axes and bifaces (Fig. 7, 8) numbering over 100 specimens are waterworn and occur in gravels lying above the Boulder Conglomerate on the highest terrace along the Soan valley. Since this terrace gravel is buried under the loessic silt of the third glaciation (Fig. 9), it is obvious that this culture must belong in that long second interglacial which is also well recorded in the adjoining Kashmir-Himalaya. Some of the specimens are identical with the crude Chellean hand-axes of Madras suggesting a regional extension of the Old Paleolithic from southern India to the Himalayan hills. The Soan complex is represented by both chipped pebbles and flakes (Fig. 10), of which the latter show prepared striking platforms and high percussion angles reminiscent of the Levallois and Clacton techniques of the Old Paleolithic in Europe. These artifacts are abundantly met with in the basal gravels of the Potwar loessic silt. Workshops are numerous along valleys and not a few of them lie in the basal layers of the loessic silt (Fig. 9). The bulk of this industry therefore was manufactured at the close of the interglacial and at the beginning of the third glaciation. The admixture of pebble-choppers and flakes of Soan type with the Chelleo-Acheulean tools (at Chauntra) and reversedly the presence of a fresh Chellean hand-axe in a workshop of the Soan people (at Adial) indicates, that both facies belong principally in the same Old Paleolithic complex. A few of the Soan tools, especially choppers, would not be out of place in the culture of Peking Man whose age as we saw was tentatively regarded as late Mindel.

In the Narbadda valley of central India the two Old Paleolithic complexes appear in association with well known mammals of the middle Pleistocene Narbadda fauna (*Elephas namadicus*, *Bos namadicus*, *Equus namadicus* etc.). Artifacts of Soan type occur already in the basal gravel with the Chelleo-Acheulean tools and dominate in the 'upper group' of the Narbadda river formation. A microlithic industry

(? Mesolithic) mainly cores, scrapers and knives made in calcedony, jasper and flint, is here found in the 'cotton soil,' a silty to loessic product of late Pleistocene times. Mesolithic tools are also known from NW India where, so far, few have been found on the surface of the loessic silt. This is the only culture which one might assign to a closing stage of the Pleistocene in India. As in China then, the Upper Paleolithic is linked with the young Pleistocene cycle 5.

To sum up from India there are known so far three major tool complexes of Pleistocene age viz a pre-Chellean in the topmost Siwalik gravels, an old Paleolithic from the second interglacial to the third glacial stages and a Mesolithic in late Pleistocene deposits. In addition there are in the Siwaliks certain fossil records suggestive of a diversified anthropoid life endowed with progressive tendencies towards Man. As in China, Man was first recorded in the Middle Pleistocene formation (cycle 4), then later at the base of the two loesses of cycle 5. However in China this loess apparently belongs to the 4th glaciation, whereas the Indian loess represents the 3d glacial stage. This difference in age of the two loesses may account for the difference in the archeologic records which is apparent in the absence of a true Mousterian culture in India. Here the culture of a Neanderthal race remains to be discovered. True Upper Paleolithic, such as Solutrean and Magdalenian is unknown in India, instead there appears a Mesolithic culture with typologic relationships to the Capsian of Syria and Africa (Paterson, deTerra 1936).

JAVA

Already Dubois (1908) had noted that the fauna of the Trinil horizon in which he discovered *Pithecanthropus erectus*, contains certain forms which are common guide fossils in Cenozoic formations of India and Java. These are specifically *Elephas cf. namadicus*, *Cervus lydekkeri*, and *Hexaprotodon namadicus*. They are found in the Upper Siwaliks which led certain paleontologists to the assumption that the Trinil horizon was of Upper Siwalik age which Pilgrim considered to

be late Pliocene or early Pleistocene. The new age interpretation of the Upper Siwaliks in India calls for a revision of such dating, it demands that the Trinil horizon and *Pithecanthropus* be of Middle Pleistocene age. That such is indeed the case has meantime been proven by von Koenigswald (1935) whose paleontologic studies resulted in a three-fold division of the Pleistocene in Java. In the preceding Pliocene, Java was still largely submerged under the sea and therefore the first three Cenozoic cycles of continental Asia are missing altogether. Significantly enough the emergence of the island falls into the time of the great Himalayan uplift which makes us suspect from the outset that the Himalayan region and Java were then already united by a similar geotectonic fate. The Old Pleistocene cycle 4, is divided into two stages, the Djétis beds and the Trinil horizon (Siwalik condition). The Djétis beds are of fluvio-lacustrine origin

PLEISTOCENE	Upper	Ngandong-beds terrace	Upper Paleolithic bone- and stone-industry <i>Homo soloensis</i>
		erosion	Early Paleolithic Chellean and Pre-Chellean
	Middle	Trinil-beds gravel and volcanic ashes	<i>Pithecanthropus erectus</i>
	Lower	Djéti-beds (fluvio-lacustrine)	<i>Homo modjokertensis</i>
PLIOCENE		marine and estuarine formations	

FIG. 11 Cenozoic sequence in Central Java

and bear an early Pleistocene forest fauna in which *Hippopotamus antiquus*, *Stegodon*, Buffalo, Tapir and *Rhinoceros sondaicus* are prominent. The only Chalicotheres, *Nestoritherium sivalense*, is an Upper Siwalik form from the Pinjaur zone. In these beds was recently found the most ancient human fossil so far known in Asia, the skull cap of an infant whom Koenigswald (1936) has provisionally called *Homo-*

modjokertensis. If further studies can confirm the early Pleistocene age of this human fossil, Man's antiquity in Asia can almost be traced back to the beginning of the Ice Age. This consideration obviously supports the contention, previously expressed, that the preceding cycles 3 and 2 deserve closest attention for coming searches for proto-human remains. Since these Cenozoic stages are practically missing in Java one is inescapably forced to assume a center of dispersal of the Pliocene anthropoids in India and China

The Middle Pleistocene or Trinil horizon, bears the remains of *Pithecanthropus erectus* in association with a few Siwalik mammals. Koenigswald has (1936 c, p 730) recently found other fossil human teeth and implements in this horizon which suggest that a higher type of man was then in existence. So far as preliminary reports allow one to judge, (Koenigswald, 1936 b) the trinil industry belongs exclusively in that Old Paleolithic tool complex of Asia to which the culture of Choukoutien and of the Soan river belong. As in India, Chellean hand-axes of the Madras type, and Levallois flakes appear here with a variety of chipped pebbles and flakes, some of which are still pre-Chellean in type while others do not permit of any sure interpretation. As far as flaked pebbles and flakes go, the Trinil culture resembles the Upper Siwalik pre-Chellean of India which is also present in the lowest Narbadda horizon. Hence it does not seem so improbable, as Koenigswald is inclined to believe, that the Trinil culture is too advanced to have been made by a man with a brain capacity of 900 ccm. It is however definitely too primitive for a Neanderthal race, and we must hope that coming researches will show us the type of man who is responsible for the Chellean culture in Java and India.

The Upper Pleistocene or Ngandong stage finally saw the emergence of a modern forest fauna in which recent forms such as *Rhinoceros sondaicus*, Muntjac, Java deer and Banteng are mixed with extinct types (*Stegodon*, *Elephas namadicus*, *Hexaprotodon namadicus* and others). In association with these fossils there have been collected at Ngandong eleven

skulls and two tibiae of *Homo soloensis* (Koenigswald, 1935, p. 4), a representative of the Neanderthal group. From the same terrace of the Solo river van Stein-Callenfels (1936) has described a culture which is partly lithic, partly ossiferous and in which one can recognize a cultural stage transitory between the Mesolithic and early Neolithic. Interesting is the presence of microlithic tools made of semi-precious stone (chalcedony), which recalls the abundance of similar microlithic industries found in southern and central India in late Pleistocene deposits (Mitra, 1927).

Both on paleontologic and archeologic grounds we must assume that migration routes existed in the younger Pleistocene between Java and the mainland of southeast Asia. This contention makes clear that Java (with India and China) is an important triangulation point in the geologic survey of the Cenozoic formations in Asia.

CONCLUSIONS

If we compare the geologic setting of Early Man in these regions we recognize that the Old Paleolithic cultures appeared uniformly during the Middle Pleistocene apparently at the close of the second glaciation and in the second interglacial (or interpluvial). With this perception there become visible two outstanding landmarks in the evolution of Man in Asia: the Pliocene period with its progressive anthropoid evolution, and the Middle Pleistocene stage with its uniform emergence of tool making races, such as Peking Man. The interval should to all appearance represent the critical phase of proto-human evolution which is the time of both climatic changes and earth revolutions.

That Old Paleolithic cultures appear uniformly in Middle Pleistocene deposits must have special reasons. This period embraces a major mountain glaciation as well as the longest interglacial (or interpluvial). From paleontologic records we know that the latter promoted migrations of mammals over wide areas and it is very probable that Early Man migrated with the herds as a hunter, thereby leaving traces of his

manual skill in widely scattered regions. If such were the case, Man as a race should have been sufficiently developed to adapt himself to changing environments. This consideration forces us to discriminate more clearly than ever between autochthonous and migratory evolutions of prehistoric cultures in Asia. In addition it focuses attention on the role which geologic factors have played in the biologic evolution of Man. This perception should orient our views and studies toward a closer cooperation of institutes and individual scholars interested in the problem of human origins in Asia.

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PLATE I



FIG. 5. Unconformity and hiatus between Upper and Middle Siwaliks at Adial (Soan valley).

B. C. = Boulder Conglomerate with pre-Chellean tools.

D. P. = Dhok Pathan sandstone.

PLATE II

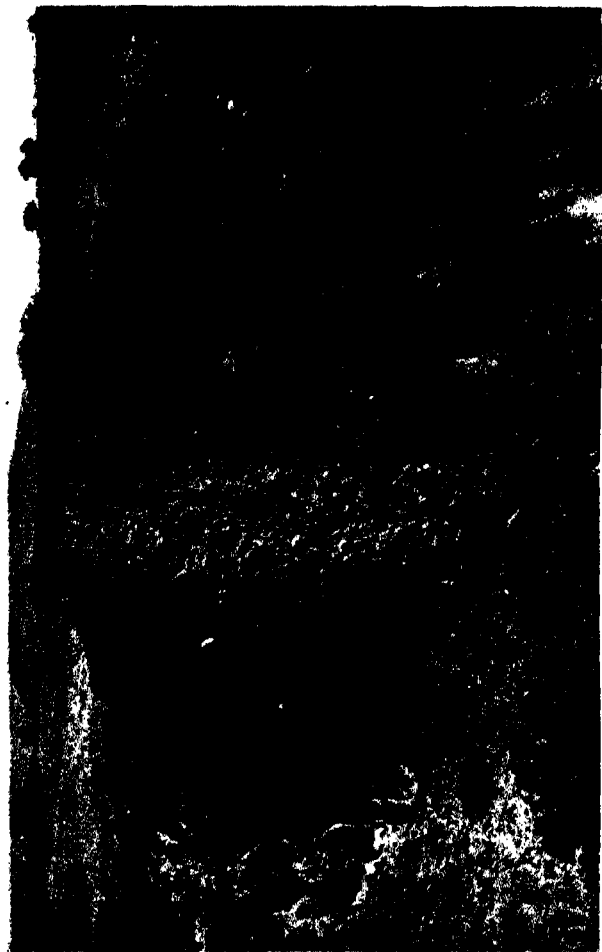


FIG. 6. Boulder Conglomerate. High angle tilting at fault-thrust near Golra (Punjab). (Photo by Dr. Teilhard.)

PLATE III

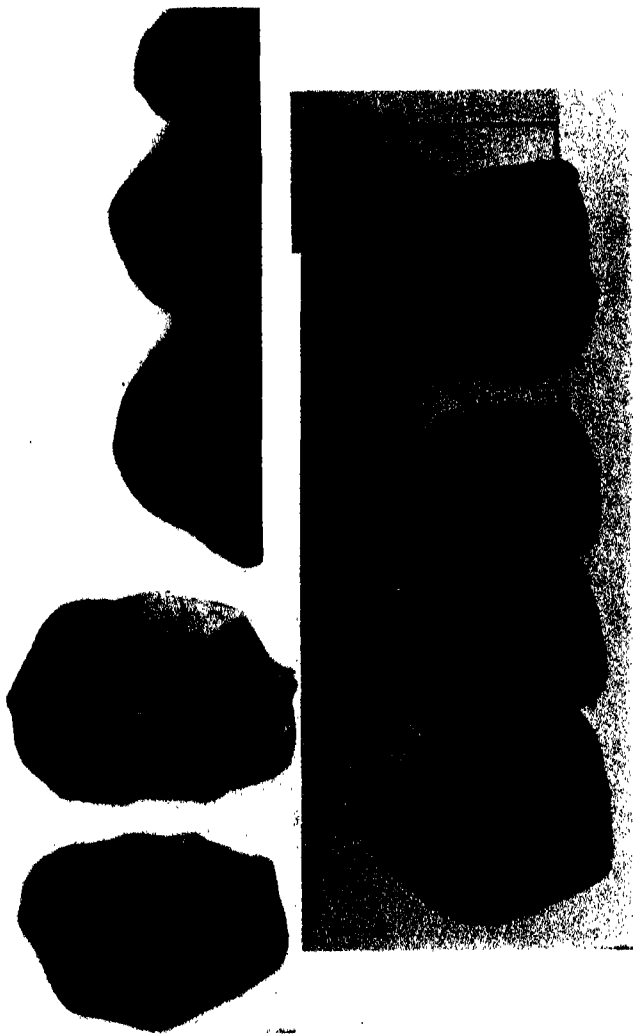


FIG. 7. Pre-Chellean (upper row) and Chellean (lower row) tools from Boulder Conglomerate and upper terrace gravel near Rawalpindi (Punjab).

PLATE IV

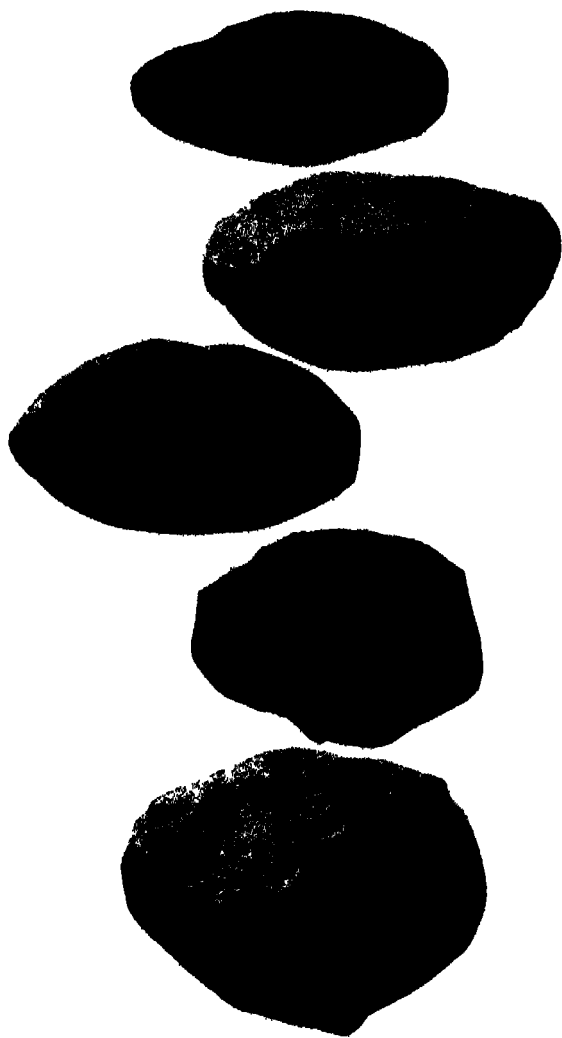


FIG 8 Chellean hand-axes (left) and Acheulean bifaces (right) from upper terrace gravel of Soan valley

PLATE V

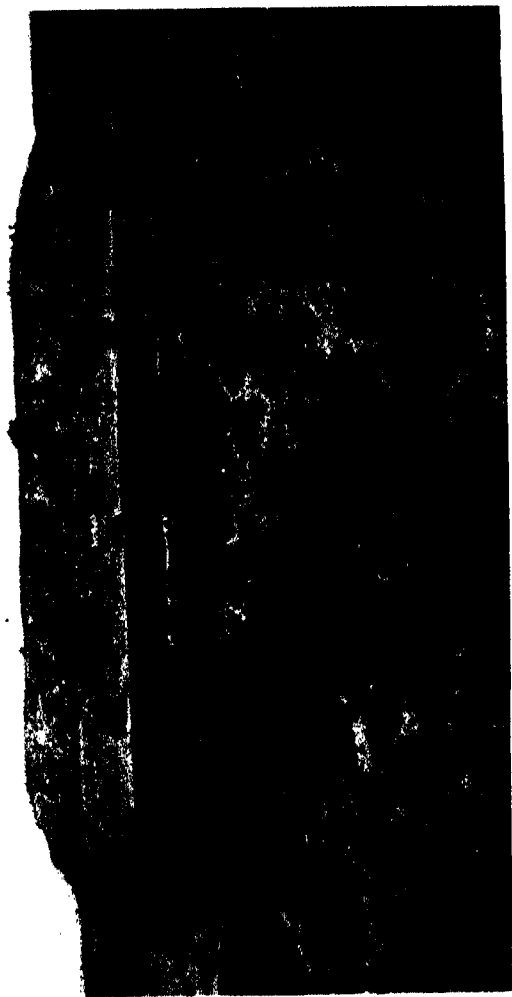


FIG. 9. Right slope of Soan valley above Chauntra.
Ps = Potwar silt; W = Level of workshops of Soan industry above cliffs (Boulder Conglomerate).

PLATE VI

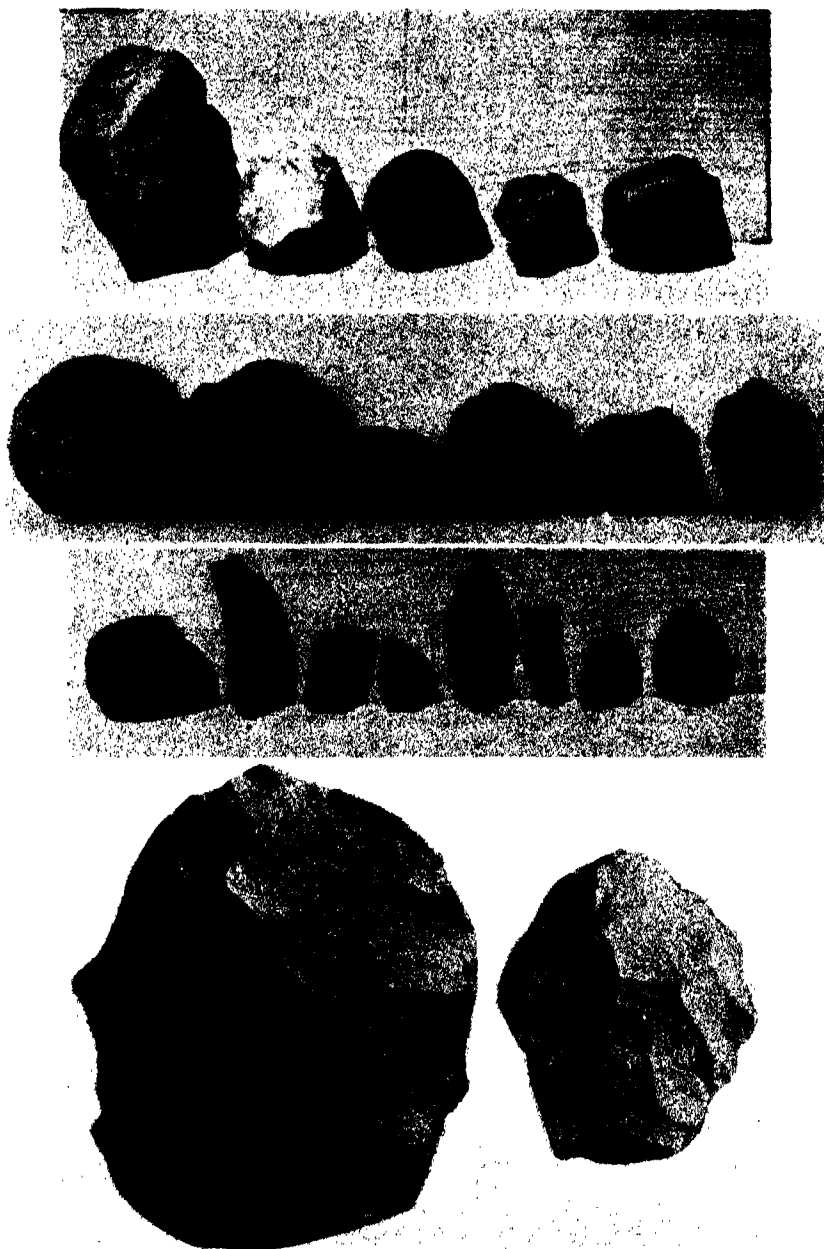


FIG. 10. Artifacts of Soan industry.
(Choppers, scrapers, flakes and cores.)

THE ASTRAPOTHERIA

WILLIAM BERRYMAN SCOTT

(Read February 7, 1936)

ABSTRACT

The Field Museum in Chicago has the only known skeleton of *Astrapotherium*, discovered by Mr F S Riggs in the Santa Cruz of Patagonia. This unique skeleton, together with a partial one of *Parastrapotherium*, formed the object of the following study.

The skeleton is one of paradoxes and contradictions, so that the interpretation of structure in explaining function is exceedingly difficult, especially because no animal now living is in the least like these extraordinary creatures. *Astrapotherium magnum*, the Santa Cruz fossil, is about the size of an Indian rhinoceros. The skull has long been known, but remains of the vertebrae and limb bones are very rare. The skull apparently indicates the former presence of a proboscis, though the relatively long neck makes this doubtful. The trunk vertebrae are extraordinarily weak for an animal of that size, and the neural spines and the transverse processes are so short and slender as to indicate that the muscles of the back were greatly underdeveloped from the modern point of view. The limbs are weak and slender and the feet proportionately very small. The fore foot has a superficial likeness to that of the elephants, and the hind foot seems to have had a plantigrade position, altogether a most grotesque assemblage of characters. The question of habits is discussed, and the conclusion reached that an amphibious mode of life best explains the unusual characters, though this conclusion cannot be regarded as certain.

THE astonishing mammals of this exclusively South American order were first made known by Burmeister in 1879, when he described and named the typical genus *Astrapotherium*. The name (from *ἀστραπή*, lightning) was given because of a supposed resemblance of the Patagonian animal to the North American perissodactyl, *Brontotherium* (from *βροντή*, thunder). He wrote: "Je propose, vu l'analogie de cet animal avec le *Brontotherium* de lui donner le nom de *Astrapotherium*" (1879, p. 517). A more inappropriate and infelicitous name could hardly have been selected, for anything less lightning-like than this strange beast cannot be imagined. The "analogie avec le *Brontotherium*" is a vague expression that might mean anything, and Burmeister's text shows that his meaning was very far from clear to himself, though it would seem that

he had some vague intention of referring his new genus to the *Perissodactyla*.

Dentition and skull were described by Ameghino, who was the first to recognize that this strange creature should be made the type of a separate order, which he called the *Astrapotherioidea*, and less than a month later Lydekker made the same proposal but with a slight difference in the form of the name, which he wrote *Astrapotheria*. It is better to use Lydekker's term, not only because it is so much less cumbersome, but also because the termination in *-oidea* is now reserved, so far as possible, for superfamilies. The skull of *Astrapotherium* is not uncommon in the Santa Cruz formation of Patagonia and the beautiful specimens in the collections of Princeton University, secured by the late Mr J B Hatcher, and of the American Museum of Natural History, collected by Mr Barnum Brown, have been fully described and figured by the writer in the Princeton *Patagonian Reports* (Vol VI) together with a few scattered limb-bones. The fore foot of an allied genus was figured by Tournouer, but the skeleton has remained almost entirely unknown, until the fortunate discoveries made by Mr. E. S. Riggs of the Field Museum, Chicago. These include a nearly perfect skeleton of the Santa Cruz genus and an extensive part of another and larger animal from the Colhué-huapi formation (or *Colpodon* Beds of Ameghino). Mr. Riggs has published a summary account of the Santa Cruz skeleton and has turned all the Field Museum material of this group over to me for "study and publication." I am greatly obliged to him for this highly prized opportunity to lift in some degree the veil that has covered this problematical group.

The simple classification needed in these studies is as follows

Order ASTRAPOTHERIA Amegh. *emend.* Lydek.

Family ASTRAPOTHERIIDAE Amegh. †

Genus 1. *Astrapotherium* Burm., Santa Cruz

2 *Astrapothericulus* Amegh., Colhué-huapi

- 3 *Parastrapotherium* Amegh , Colhué-huapi & Deseado
- 4 *Astraponotus* Amegh , Musters
5. *Albertogaudrya* Amegh , Casa Mayo

ASTRAPOTHERIUM Burm

(Pls. I-VII)

As the dentition and skull of this genus are already known with much completeness, only a summary account of them will be given here, sufficient to bring together the more important structural facts concerning one of the strangest and most mystifying mammals that palaeontology has revealed

DENTITION

The dental formula is $i_3^0, c_1^1, p_1^2, m_3^3$. Of the upper incisors no trace remains, unless some small pits in the premaxillae are the remnants of alveoli. The *canine* is a large and formidable tusk, open at the base and, evidently having grown from a permanent pulp, the tooth is somewhat curved, though the extruded portion is nearly straight and is of trihedral cross-section, with broad anterior face, narrowing to a bluntly rounded hinder edge. Enamel covers the sides of the tusk, but is absent from the anterior face and sometimes from the posterior edge also. Where present, the enamel is obscurely ridged longitudinally. The distal end of the tooth is obliquely truncated by the abrasion of the lower canine.

The *upper premolars* are very much smaller and less complex than the molars, p_2 is the smaller and simpler and has but a single recognizable external cusp, though the outer surface is divided by a convex vertical rib. The single internal cusp is separated from the external one by a valley, but confluent with it anteriorly and posteriorly; the enamel is thick and covers the crown uninterruptedly. The fourth premolar (p_4) is like p_2 , but is considerably larger and the outer rib is more prominent, the inner cusp is conical and the valley is open behind.

The *upper molars*, in an unworn state, have much resemblance to those of the contemporary toxodonts and have similar high and curved crowns, though in much less extreme degree, and roots are formed at an early stage. The external wall of the crown is much as in one of the rhinoceroses, and near the anterior border is a prominent convex vertical style, with a broad, shallow groove in front of it. Two transverse crests are given off from the outer wall, the anterior crest, which forms the front wall of the tooth, is so curved that its inner portion is parallel with the external wall, the posterior crest is straight and much shorter than the anterior, there are two valleys, the principal one between the transverse crests and an accessory one enclosed between the posterior crest and the outer wall. A large oblique spur runs from the outer wall to the hinder crest, enclosing a deep, enamel-lined pocket. A much smaller spur arises from the outer wall behind the posterior crest. The third upper molar has the trigonal shape general among the rhinoceroses, the posterior transverse crest being reduced to a mere rib on the inner side of the wall, the long anterior spur ends freely behind and there is no posterior valley.

The *lower incisors*, six in number, which are arranged in a transverse curve, differ somewhat among themselves in size and shape and undergo great changes of appearance with the progress of abrasion, they all have broad, thin, spatulate and procumbent crowns. Each crown is partly divided into two lobes, on the lingual and buccal, or dorsal and ventral sides, is a shallow, median groove and, on the free margin of the tooth, these grooves unite in a median notch, which is very variable in depth. On each side of the notch the free margin has a slit, where the enamel of dorsal and ventral sides fails to unite. The differences between these teeth are unimportant.

The *canine* is a large tusk, which is curved almost in a semicircle and, to all appearances, continued to grow throughout life, for, even in very old animals, the base is widely open, a condition which is not found in any of the preceding genera.

of the family. The cross-section differs from that of the upper tusk, being broad behind and narrowing to a thin edge anteriorly, the external face is convex and the inner side is convex for most of its breadth, but, anteriorly, there is a wide, shallow groove, following the anterior border, which is slightly inflected. On the hinder face of the tusk the enamel is lacking, exposing a broad band of dentine and, in several individuals, the enamel of the inner and outer sides is separated by a slit along the anterior border, which, in other individuals, is completely covered with enamel. A very frequent and puzzling feature is the presence of two or more transverse grooves on the anterior edge of the tusk, at points where no other tooth could have reached it, the grooves must have been made by rubbing against some external object, though it is difficult to imagine what such objects could have been.

The likeness of the tusks of *Astrapotherium*, in form and mode of wear, to those of the Hippopotamus is very striking.

The only *premolar* in the lower jaw is the fourth, it is very much smaller than the lower molars, but similar to them in form, which is bicrescentic. The two crescents are, however, much more nearly equal in size and the valleys are far shallower. The internal cingulum is much more prominent.

The *molars* vary greatly in size, in accordance with age and amount of abrasion. The crown consists of two crescents, of which the hinder one is much the larger and lacks the anterior horn, its place being taken by the internal pillar, which is so characteristic of South American ungulates. The two crescents are separated by a deep cleft, which is gradually obliterated by wear, making the crescents confluent and forming a lake from the fossette between the pillar and the hinder horn of the anterior crescent. Enamel is absent from the anterior face of mI and, on the approximate faces of all, it does not extend to the base of the crown and is therefore absent on those faces in well-worn teeth.

Milk Dentition.—According to Ameghino, the temporary formula is dp_3^4 . The lower milk-incisors are like the per-

manent ones, except in size. The third temporary upper premolar (dp₃) is very small and, when worn, has no determinable pattern, dp₄ is much larger than dp₃ but much smaller than the first true molar (m₁) which it resembles in form. The three lower temporary premolars are bicrescentic and molariform

SKULL

(Pl III)

Astrapotherium had one of the most grotesque forms of skull that has yet been brought to light. There are very considerable differences in skull form and structure between the various individuals, but these are chiefly due to differences of age and sex. That some of these differences are specific is probable, but, so great is individual variability, that the discrimination of species is well-nigh impracticable. The peculiarities of this remarkable skull are best brought out by a preliminary survey of the different points of view, side, top, base, front and rear.

A Side-view—Seen from the side, the skull is very striking for the great elongation of the cranial region and the shortening of the facial. With minor sinuosities, the upper contour of the skull is nearly horizontal, rising from the occipital crest, it dips slightly and then rises into the great dome of the forehead, thence descending forward, it is once more raised by the very short, upturned nasals. The orbit is small and has a very inferior position, it is clearly defined by the post-orbital processes of frontal and jugal, but not entirely closed behind. The zygomatic arch is very long, but not very stout. The short facial region is divided into two parts, (1) the vertical portion of the maxillary, which carries the cheek-teeth, and (2) the sheath-like and convex alveolus of the upper tusk, which gives a certain elephantine likeness to this part of the skull. The vestigial premaxillae are not visible from the side, being concealed by the tusk. The most noteworthy features of the mandible in side-view are the shallowness of the horizontal ramus and the long edentulous space between canine and foremost premolar.

B. Top-view.—This is no less peculiar, the brain-case is of small capacity and its roof is a narrow isosceles triangle, the base of which is the line joining the post-orbital processes of the frontals and the apex is the point of junction of sagittal and occipital crests. In front of the base-line the face narrows gradually forward to the abrupt constriction in advance of the orbits. The sagittal crest, though very high, is short, soon dividing into the temporal ridges, which diverge very gradually forward into the post-orbital processes. The great dome of the forehead, caused by hypertrophied frontal sinuses, is especially conspicuous in this view. The roots of the zygomatic processes of the squamosals are very broad antero-posteriorly, in consequence of which the temporal openings have no great extension. The arches arise well forward, much of the cranium projecting behind them. The vestigial nasals expose most of the anterior nares.

C. Base-view—The posterior part of the skull is narrow, a great difference from all the Notoungulata, in which this region is very broad. The posterior nares are far forward and the large tusks and vestigial premaxillae make this view extremely peculiar.

D. Front-view—The views from the two ends are the strangest of all, seen from the front, the most striking feature is the great frontal dome, and next is the high, narrow, hour-glass-like shape of the anterior nares. The small and widely separated orbits are low down on the sides of the skull. The vestigial nasals and premaxillaries and the large tusks, with their rounded sheaths add much to the grotesque effect.

E. Rear-view—From behind, the occiput is narrow and rather low, as the squamosals have no such inflated chambers as broaden the occiput in the Notoungulata. There are no mastoid processes, only heavy and not very elongate par-occipitals.

Taking up the details of skull-structure, it may be observed that the *basi-occipital* is moderately long, heavy, broad behind and narrowing forward. The *exoccipitals* are relatively small and form but little of the inion, though they alone are

involved in the large occipital condyles, the paroccipital processes are moderately long and very broad, thin, and antero-posteriorly compressed, distally they contract to blunt points. The paroccipitals are closely applied to the post-tympanic processes of the squamosals, excluding the mastoids from the surface. The *supra-occipital* is very large and forms most of the inion, the free margin of the bone is raised into a thin and prominent occipital crest, which is separated from the dorsal border of the zygomatic arch by a constriction at the suture between ex- and supra-occipitals and above it the occiput broadens very gradually, the crest describing a regular curve. The parietals are long and wide, and carry a very high sagittal crest, which is short and broadens anteriorly into the triangular area above described.

The *squamosal* has a large cranial portion, which ceases at the occipital crest and is not visible from behind. Between the post-tympanic and post-glenoid processes is a wide space in which must have been the auditory meatus. No tympanic bulla has been found and, presumably, it was not ossified, in the large fossa which is left open by the absence of the tympanic, appears the short and heavy tympano-hyal, attached to the post-glenoid process, this process is somewhat tapir-like in form, being at the base a broad transverse ridge, but, distally, it contracts more and is thicker antero-posteriorly than in the tapirs. On the front side, the process bears a facet for another surface on the postero-internal side of the mandibular condyle. The glenoid surface, which can hardly be called a cavity, resembles that of a rhinoceros in being slightly raised and in being rather concave transversely, convex antero-posteriorly. The zygomatic process is long and has a very broad root, or origin, which extends back as a horizontal shelf over the post-glenoid and post-tympanic processes. The free antroverted part of the process is compressed and plate-like and rather slender; it reaches forward almost to the orbit, overlapping the jugal in a very long suture. The *jugal* is of similar form, compressed and slender and extending almost to the glenoid cavity; the postorbital process is low, but distinct.

The *frontals* are very large, much exceeding the parietals both in width and length; they widen anteriorly, becoming immensely broad over the orbits, where the whole forehead rises in a convex dome. Fractured specimens show that this highly characteristic dome is filled with a complicated system of communicating cells. There is no rugosity, nor any sign of attachment for a horn, though there is a certain likeness to the much more prominent and definitely circumscribed horn-base of *Elasmotherium*, the gigantic Pleistocene rhinoceros of Europe and Asia. Anteriorly, the frontals are deeply notched for the nasals. The temporal fossae are exceedingly long and, for nearly their whole length, they have a slightly overhanging superior boundary, formed by the skull-roof and even by the sagittal crest. The fossae have deeply concave walls throughout, but diminish anteriorly in dorso-ventral height.

The *nasals* are reduced to vestigial proportions, they are extremely short, though longer than would appear at first sight, because of the deep notch of the frontals in which they lie, the free portion, in advance of the frontals, is very short indeed and sharply upturned, ending in bluntly rounded tips. The nasals articulate only with the frontals and are far removed from the maxillaries.

Like the nasals, the *premaxillae* are vestigial, they are edentulous and have no ascending rami, articulating only with the maxillaries. In the fully adult skull, the two bones are fused together and imperforate, as there are no incisive foramina, the naso-palatine nerves probably descended through the notches between maxillaries and premaxillaries. There is considerable variety of shape in the premaxillae of different skulls, for the most part, these bones are thick, bluntly rounded at the free ends, very short and convex on the ventral side. Posteriorly, the premaxillaries gradually contract to the posterior end and are firmly wedged into a triangular space, formed by the divergence of the maxillary palatine processes. The significance of the extremely reduced nasal and premaxillary bones will be discussed at the end of the description of the skull.

The *maxillaries* are very large and, together with the frontals, make up nearly the whole of the short facial region. The sub-orbital portion is low, but forms the broad floor of the orbit and extends well behind it, where it is swollen by the large alveolus of the third molar. In front of the orbits the face is sharply constricted, which gives the eye-sockets an unusual position, as is best seen when the skull is viewed from the front. The infra-orbital foramen is small and hardly visible in side view; it has a very elevated position, close to the anterior boundary of the orbit and opposite its middle, or even, in some instances, its top. The pre-orbital part of the maxillary is high and concave and extends up to a junction with the frontal. The large sheath of the tusk makes a prominent convexity in front of the cheek-teeth and curves back above them. The palatine processes are long and narrow, deeply notched anteriorly by a broad, V-shaped incision, to receive the premaxillaries, but these bones do not fill the entire breadth of the notch in front, leaving on each side a narrow slit, which probably served for the transmission of the naso-palatine nerves. The hard palate is of nearly uniform width and deeply concave transversely. In the edentulous space before the cheek-teeth, the boundary of the soft palate is distinctly indicated.

The *palatines* are narrow, elongate bones, which extend forward to a line opposite the middle of m_1 , where they form nearly the whole breadth of the bony palate, transversely, they are slightly convex, with a median ridge along the line of suture and are united for some distance behind the last molars (m_3). From the posterior border, a deep notch on each side invades the palate between the palatine bone and the alveolus of the last molar; in the young skull, in which m_3 has not been erupted, the notch is bounded externally by the alveolus of m_2 . The posterior nares are rather small and their ventral opening is V-shaped.

The *mandible* is very peculiar in certain respects; the ascending ramus is relatively low, broad antero-posteriorly, and has but a slightly concave external surface, the masseteric

fossa being very ill-defined. The angle is regularly rounded and somewhat thickened, with rugosities on the inner side. The condyle is very broad transversely, with a slight inclination downward and inward, on the posterior side of the inner end is a well-marked facet for the post-glenoid process. The coronoid process is high and nearly erect, with very slight recurvature, though the process is high, the sigmoid notch is shallow, for the condyle is sessile. The *lineae obliquae*, both internal and external, are prominent, enclosing a moderately deep fossa.

The horizontal ramus is very long, shallow dorso-ventrally, but very thick transversely, with strongly convex external surface, bulging out beyond the plane of the cheek-teeth, while the lingual side is nearly flat. The two rami of the jaw are co-ossified in a long narrow symphysis, which posteriorly, is deeply concave on the dorsal side; anteriorly, between the canines and behind the incisors, it becomes very shallow. The chin slopes forward and upward gradually and is, in fact, almost procumbent, its surface is rough and is pitted by many small vascular foramina. The mental foramina, below the edentulous space between canine and premolar, vary in number, usually there are two conspicuous openings, one near the premolar, the other near the canine.

The skull of *Astrapotherium* is of very difficult interpretation because of the many seeming contradictions in both skull and skeleton. The extreme shortening of the nasals and the character of the nasal passage immediately suggest a proboscis in the living animal, but opposed to this suggestion is the length of the neck which would seem to render a proboscis needless. An alternative hypothesis would be to infer the presence of an inflated muzzle, somewhat as in the Moose (*Alce*) or rather as in the Saiga Antelope (*Saiga tatarica*), but in the Moose and even more conspicuously in the Saiga, the premaxillaries extend forward as far as the lower incisors and support an elastic pad, against which those incisors bite. In *Astrapotherium*, on the contrary, the premaxillae are so short that the mandible, with its incisors, extends far in front of

them and, to all appearances, there was nothing against which these teeth could bite. Nevertheless, the lower incisors must have been in constant use, for they show abrasion conspicuously and often, in very old animals, they are worn down to mere stumps. Obviously there must have been some firm, elastic surface against which these teeth could bite and the analogy of the Miocene and Pliocene mastodonts, which had long, cutting *lower* tusks, suggests that it was only the ventral side of a proboscis which could have afforded the necessary opposition for the lower incisors

By an unfortunate oversight I suggested in my account of the Astrapotheria in the *Patagonian Reports*, that the premaxillae probably supported the pad for the lower incisors, forgetting that these teeth were far in front of the premaxillaries and could not possibly have reached them. The unshortened neck is not a fatal objection to the assumption that these animals had a proboscis, for the tapirs have a neck relatively as long. I am inclined, therefore, to believe that Mr Horsfall's restoration of the head of *Astrapotherium*, as published in my *History of the Land Mammals of the Western Hemisphere* (p. 510), gives a fairly adequate conception of this strange creature, when in life.

VERTEBRAE AND RIBS

(Pls. I, II, IV, Fig. 1)

The only complete vertebral column so far obtained is in the Field Museum skeleton (No. P. 14,251), in which the column is entire, back to and including the sacrum, with doubt as to one lumbar, no caudals are preserved

The vertebral formula is: C7, D19, L?6, S \pm 5. The neck is moderately elongate, measuring considerably less than the skull, mandible and lower incisors included, apparently the animal was able to reach the ground to graze, or to drink, without crouching or straddling. The *atlas* is very broad and has extensive transverse processes, which are widest at the posterior angle, with simply curving free border. The processes are extended behind into bluntly rounded tips, which

project well behind the plane of the posterior cotyles. The anterior cotyles for the occipital condyles are large, deeply concave and widely separated dorsally by a broad emargination of the neural arch, ventrally, they are nearly approximated, with a space of $\frac{1}{2}$ to $\frac{3}{4}$ of an inch between them. The inferior arch is thin, convex on the ventral side, with small, hardly more than vestigial, hypapophysial tubercle on the hinder border. The neural arch has a vestige of the spine in the form of a very low ridge. The foramen for the first spinal nerve opens into a remarkably large fossa on the dorsal side of the transverse process and at the bottom of this fossa is the atlanteo-diapophysial foramen. The posterior cotyles for the axis are large, oval and nearly flat surfaces.

The *Axii* is much the largest vertebra of the neck, the centrum is anteriorly broad and depressed, narrowing and thickening posteriorly, so that the hinder face is subcircular and concave. The articular surfaces for the atlas are very broad, projecting far externally to the sides of the centrum, which is keeled, both on the ventral side and along the floor of the neural canal. This canal is high and rather narrow, the spine is very large and of almost quadrate contour when viewed from the side, projecting but little in front of or behind the pedicles of the neural arch, the free border of the spine is very thin for the anterior two-thirds of its length, the hinder third thickening rapidly to the posterior end, where it forms a projection overhanging on each side, the pedicles of the neural arch are very broad from before backward, and the post-zygapophyses are large and flat, presenting ventrally. The transverse processes are long, compressed and light and extend almost directly backward; they are perforated at the base by unusually long vertebrarterial canals.

The *Third Cervical* is much shorter than the axis, the pre- and post-zygapophyses of each side are near together, nearly flat and present almost dorsally and ventrally, though the anterior pair is slightly oblique. The neural arch is broad, and flat on the dorsal side, a spine was present but is broken away. The transverse processes are broad and are continued

down into very large inferior lamellae, which project obliquely backward and overlap the anterior part of the fourth vertebra, the bridge over the canal for the vertebral artery is broader than in the succeeding vertebrae

The *Fourth Cervical* is like the third except that the bridge over the arterial canal is narrower and the inferior lamella is broader proximo-distally and shorter antero-posteriorly, the spine is broken.

The *Fifth Cervical* differs from the fourth only in small details, such as a narrower bridge and smaller inferior lamella, and the *Sixth* differs in much the same way from the fifth.

The *Seventh Cervical* has, as usual, imperforate transverse processes, which are short and thin, and no inferior lamellae.

When the seven vertebrae of the neck are seen from the ventral side in their natural connections, they have a decided resemblance to those of a horse, though the neck is markedly shorter. The centra are deeply concave behind, the anterior faces nearly hemispherical and the articulations are thus ball-and-socket joints, almost as completely so as in the modern horses. The transverse processes also have a general resemblance to those of the equine vertebrae. There is, of course, no question of relationship between the *Astrapotheria* and the horses any more than there is between *Macrauchenia* and the camels because of a decided similarity in the cervical vertebrae (Pl. IV, Fig. 1.)

The *Dorsal Vertebrae* have the centra all concealed in the matrix, but the arches and spines are free. The anterior dorsals are short and have such remarkably short and weak neural spines that there can have been no indication of a shoulder hump. The spines all incline backward, but the steepness of inclination diminishes posteriorly and, in the hinder part of the thorax, the spines take on a lumbar-like shape, with broadened and thickened tip. The transverse processes are prominent in the anterior dorsal region and bear large, concave facets for the rib tubercles; processes and facets diminish posteriorly in the usual fashion. The zygapophyses of the last three dorsal and all the lumbar vertebrae are of the

cylindrical, interlocking type like those of the Artiodactyla and some perissodactyls also

The *Lumbar Vertebrae* are unusually simple, having no metapophyses or anapophyses, and the transverse processes are remarkably weak, being short, narrow and thin. The neural spines of the lumbar continue the backward inclination of the dorsal spines, but the posterior ones are nearly erect, they are all thickened and roughened at the free end, and the hindmost ones have the thick, rugose tips bifid at the posterior border

Taken together, the trunk-vertebrae are astonishingly weak for so large an animal, as large, indeed, as the Indian Rhinoceros, and not the least surprising feature is the shortness and slenderness of all the neural spines and of the lumbar transverse processes. In ungulates generally, the cervicals have larger, broader and heavier centra than those of the lumbar, but in *Astrapotherium* the disproportion is uncommonly great. The dorsal muscles, especially the *longissimus dorsi*, must have been very weak, and how the great head was supported and moved, it is difficult to see, unless the lateral muscles of the neck, such as the *longus colli*, were attached to the scapula. The even more extraordinary *Pyrotherium*, of the antecedent *Deseado* formation, has similarly short neural spines in the trunk-vertebrae, and the great size of the skull in that animal makes the problem of head-support still more puzzling

The *Sacrum* consists of at least four and probably of five coalesced vertebrae, three of which have pleurapophyses and support the pelvis. In the posterior part of the sacrum the vertebrae become so thin as to make it probable that the tail was short

The *Ribs* show no very striking peculiarities, the first four pairs are short, broad and straight, especially the first pair. Behind the fourth, the ribs become slender and rod-like, remarkably so for so large an ungulate; the maximum length is attained by the eighth, behind which the ribs become progressively shorter and more slender. The thorax is very long,

but of no great breadth or depth, as is indicated by the length and curvature of the ribs. The lack of costal cartilages, sternum and sternal ribs makes it impossible to determine accurately the capacity of the thorax, but, as shown by the ribs and the shape of the pelvis, it was evidently not very great.

LIMB GIRDLES

If *Astrapotherium* possessed clavicles, as *Homalodotherium* seems to have, no trace of them has been found and their absence from so complete a skeleton as that of the Field Museum is good evidence that they did not exist in the genus. This conclusion is supported by the ginglymoid elbow joint.

The *Scapula* is of unusual form, its proximal third, or half, narrowing upward and making the suprascapular border very short, rounded and almost pointed, giving to the blade a curiously mitre-like shape. The spine is almost median in position, but the post-spinous fossa is somewhat broader than the prespinous. The neck is broad and the coraco-scapular notch is hardly more than indicated, the glenoid cavity is an elongate oval and quite deeply concave in the antero-posterior dimension. The coracoid is inconspicuous and its limits cannot be made out. The spine is the most remarkable feature of this curious bone; increasing in height downward, its distal portion becomes very prominent. The border of the spine is wide and projects both before and behind beyond the vertical portion and terminates distally in an immensely expanded, irregularly shaped acromion, unlike that of any other mammal with which I am acquainted. There is no smallest indication of the metacromion, a lack which is unusual among Santa Cruz ungulates.

The *Pelvis* has considerable resemblance to that of the Santa Cruz toxodont *Nesodon*. The ilium has a contracted peduncle and expands suddenly into a broad, simply concave gluteal surface; the ischium and pubis have been lost from this individual, but are known in *?Parastrapotherium* of the Colhué-huapi stage. It is thus impossible to say whether the sacral bar, which in *?Parastrapotherium* extends back to the ischium, was present in the Santa Cruz genus.

LIMBS

The limbs are remarkably short and weak and are out of all proportion to the length of the trunk, one of several features which suggest that this genus may have been more or less aquatic in habits. The proportionate lengths of body and legs are not unlike those of the Hippopotamus, but in the latter the limb-bones are relatively shorter and stouter than in the Santa Cruz genus.

The *Humerus* is relatively elongate, much more so than the forearm bones and but little shorter than the femur. The head is large, strongly convex and projects prominently behind the plane of the shaft. The external tuberosity is very large and rugose, rising well above the level of the head, but the internal one is missing on both sides; it may be seen, however, that the bicipital groove is broad, shallow and undivided. The shaft is slender proportionally, but is given an undue appearance of thickness by the deltoid ridge, which extends down for nearly the whole length of the shaft, the ridge is not very prominent and dies away toward the distal end. The distal portion of the shaft is relatively narrow, having no definite supinator ridge, internal epicondyle or foramen. The trochlea is of simple, pulley-like shape and its whole anterior breadth is covered by the radius. The anconeal fossa is very large and deep (Pl VI, Fig 1)

In appearance and proportions the forearm bones are not unlike those of the contemporary toxodont, *Nesodon imbricatus* and, though actually considerably longer than in that species, they are somewhat shorter and more slender relatively to the length of the skull. The two bones differ in stoutness, the ulna being distinctly heavier, and they are in contact only at the two ends, making the narrow radio-cubital arcade continuous throughout.

The *Radius*, like all the limb-bones, is short in proportion to the length of the neck and trunk, and except at the two extremities is relatively slender. It is considerably shorter than the humerus in the proportion of rather more than 2/3, which is not far from the ratio of length between tibia and

femur. The proximal end is broad and covers the whole width of the humeral trochlea, with which it interlocks, preventing any but a ginglymoid motion.

The joint between humerus and radius is in marked contrast to that seen in *Homalodotherium*, in which the head of the radius is so nearly discoidal as to suggest that in life the fore foot had considerable power of rotation.

In *Astrapotherium* the articular surface for the humerus is in two portions, an inner concave part and an outer more saddle-shaped one, the anterior proximal border of the outer is raised considerably higher than that of the inner part. The anterior border thus describes a sigmoid curve, concave internally and convex externally. The shaft has an irregular shape, slender proximally and broadening gradually to the distal end, which is decidedly the heaviest, most massive and rugose portion of the bone, especially in the dorso-palmar dimension. The surface for the carpus is of sub-circular shape, with no sign of demarcation between the facets for the scaphoid and lunar.

The *Ulna* is much heavier than the radius, especially in the antero-posterior diameter. The articulation with the humerus is, except in the sigmoid notch, almost entirely external, on which side the humeral facet of the ulna extends forward outside of the head of the radius, making a continuous articular surface of more than a semi-circle, while the internal portion is largely replaced by the head of the radius. The coronoid process is prominent, projecting into the deep anconeal fossa of the humerus. The olecranon is long and extends proximally in line with the shaft, not projecting behind it; the straight posterior border passes into that of the shaft with hardly any change of direction. The anterior border, on the other hand, is oblique, as the olecranon broadens above the coronoid process; the free end of the process is moderately thick and rugose and from it, on the inner side, there passes a broad deep channel, with raised anterior border, running distally and opening inside of the internal ulnar surface for the humerus. This channel has, in some degree, been modified by crushing, but it is difficult to say how far.

The shaft of the ulna is heavy and of the ordinary trihedral form, tapering moderately to the distal end. The carpal surface is narrow and convex, sloping downward to the external side, the ulna appears to rest upon the lunar as well as upon the pyramidal.

The *Femur* is the longest of the limb-bones, measuring 22 inches in extreme length, as compared with 19½ inches for the humerus. Seen by itself, the thigh-bone appears to be decidedly elongate, yet, for an animal of 9 or 10 feet in length, it is relatively short. The head is large, of very regular shape and forms more than a hemisphere, with shallow pit for the round ligament. The great trochanter can hardly be said to exist, it is nothing more than the roughened proximal end of the femoral shaft, not rising to the level of the neck and, consequently, there is no sigmoid notch between trochanter and head, but the digital fossa is deep. The second trochanter is prominent and extends into a long ridge, which is of unusual proximo-distal length. There is no third trochanter, unless a roughening of the external border of the shaft should be regarded as a remnant of it (Pl VI, Fig 2)

The shaft is antero-posteriorly compressed and flattened, in part the result of crushing, but by no means entirely so. Though flattened and wider than thick, this shaft is not actually broad, not nearly so much so, as it is, for example, in *Homalodotherium*. At the distal end the shaft is curiously widened and a heavy, not very rugose mass projects outside of the external condyle. The rotular groove is broad and shallow and has very low borders, but is carried upon a prominence from the shaft. The condyles differ notably in size and shape, the internal one being considerably larger and projecting farther backward.

The femur which Gaudry figured¹ as that of *Astrapotherium* (i.e. *Parastrapotherium*, a name which he did not recognize) was incorrectly identified and evidently belonged to *Asmodeus*, the Deseado genus of the Entelonychia. The tibia in the same figure is also mistakenly referred, though I

¹ *Ann de Paléontologie*, T I, p 19, Fig 29

am unable to place it, as it is unlike any tibia from the South American Tertiary with which I am acquainted. It cannot have belonged to any of the Entelonychia, the tibia of which has very different and highly characteristic form, unless, as is possible, *Asmodeus* should have had very different leg-bones from those of *Homalodotherium*, and the tibia of Gaudry's figure should be assignable to the former genus. However, this does not seem to be at all probable.

The *Patella* is very elongate proximo-distally, but rather narrow and remains of nearly the same width throughout, becoming much thinner in the distal portion. The anterior, exposed surface is roughened and finely striated with irregular longitudinal grooves. The articular surface for the femoral trochlea is moderately convex transversely and the whole bone is decidedly curved, a feature which is made necessary by its length, and has convex anterior and concave posterior faces. The distal end is abruptly rounded off, not bluntly pointed in the usual manner.

The bones of the lower leg are straight and slender and exceed but little in length those of the forearm, of course, not including the olecranon, which forms no part of the effective length of the ulna.

The *tibia* is straight and, like all the limb-bones of this skeleton, is relatively slender and, in general appearance, has a curious resemblance to a human shin-bone. The proximal end is broad and thick and may fairly be called massive, the prominence in which the patellar ligament is inserted is very rough. The surfaces for the femoral condyles are unequal, the internal one being larger, more extended antero-posteriorly and more concave, the external one is smaller and flatter. There can hardly be said to be a tibial spine, though the approximate edges of the surfaces for the femoral condyles are somewhat raised. The shaft has been so crushed as to reduce its width considerably, especially at the proximal end, where the outer wall of the bone has been driven inward. Comparison with the uninjured tibia of *Parastrapotherium* shows that much of the slender appearance of this bone in the Santa Cruz

fossil is due to this crushing, the antero-posterior thickness has not been reduced. The cnemial crest is prominent above and runs down three-fourths of the length of the shaft before dying away altogether; its broad proximal portion is roughened by fine longitudinal grooves and ridges in much the same fashion as the free border of the scapular spine.

The distal part of the tibial shaft is so twisted in appearance that, when the attachment for the patellar ligament and the femoral surfaces are directly in front of the eye, the distal end is oblique and the internal malleolus is almost as much posterior as lateral in position. This unusual feature is normal and not due to distortion, as is made clear by the tibias of *Parastrapotherium*, which are not crushed or distorted in any way, yet show the same remarkable twist, the significance of which is open to question.

The surface for the astragalus is almost flat, though very obscurely divided into shallow internal and external concavities; there is no definite intercondylar ridge or anterior tongue. In these respects, the bone is like the tibia of an elephant, or one of the Amblypoda, but is, of course, very much less massive. The internal malleolus is very conspicuous, not long, but thick and heavy; the articular surface for the astragalus is continued down over the distal end, where it fits into a deep fossa on the inner side of the astragalar trochlea.

The *Fibula* is straight and rather slender, though it cannot be called reduced in any sense. The proximal end, which is but little expanded, carries an oblique facet for the tibia, the shaft is of irregularly trihedral shape, which is produced by the very prominent interosseous crest, and the external surface is remarkably flat. The distal end is much more enlarged than the proximal one and forms a thick, broad, rugose and massive external malleolus, on the tibial side of which is a large, concave surface for articulation with the astragalus, but there is no contact with the calcaneum. By the above-mentioned twist of the tibial shaft the distal end of the fibula is rotated toward the dorsal side, as the inner edge of the tibia is turned to the plantar side.

FEET

The *Manus*, at a casual glance, might readily be mistaken for that of an elephant, or an amblypod, such as *Uintatherium*, but, when carefully examined, is seen to be unlike the fore foot of any other known group of ungulates. The manus which Ameghino attributed to *Pyrotherium* was shown by Tournouer and Gaudry to be assignable to *Parastrapotherium*, a reference which is fully confirmed by the Chicago skeleton of *A. magnum*, which forms the chief subject of this paper. With this skeleton the feet are associated in an entirely unequivocal manner. (Pl V, Fig. 1.)

The *Carpus* is short proximo-distally and very broad transversely, the width being almost exactly double the vertical height, and the various carpals have a massive, block-like appearance. In the details of form, and modes of inter-articulation, however, they are very peculiar and unlike the corresponding elements of any ungulate outside the limits of this order. Just what may be the significance of these peculiarities, can hardly be estimated until the feet of the Casa Mayor astrapotheres, such as *Albertogaudrya*, shall have been recovered.

The *scaphoid* is so peculiar and of such irregular form that it is difficult to give any adequate conception of it by description alone. Compared with most of the other carpals, it is relatively high and narrow, the dorsal face is broad, but, posteriorly, the bone is abruptly constricted, so that, on the palmar side, the proximal moiety is hardly one-half as wide as the dorsal face, while the distal moiety is of nearly the same width, front and back. The dorsal face is made very concave by the projection of the articular surfaces, especially of the proximal one, the dorsal border of which is an overhanging ridge. The articular surface for the radius is slightly convex transversely, strongly so palmo-dorsally; the dorsal two-thirds of its depth is broad, the palmar one-third abruptly narrowed by the constriction above mentioned. Contact with the lunar is by a narrow, plane surface near the dorsal border, the distal third of which is a very narrow band. The constriction

above mentioned prevents proximal contact between scaphoid and lunar on the palmar side. The distal end of the scaphoid is irregularly pyriform, narrow on the ulnar, broadening toward the radial side. The articular surface which covers the whole distal end is feebly convex and is obscurely divided into facets for the trapezium and trapezoid. The scaphoid does not rest upon the magnum, but has merely a lateral contact with it.

Except in the proximo-distal dimension, the *lunar* is much larger than the scaphoid and, indeed, is the largest of the carpal elements. The dorsal face is very broad and low, the palmar face much narrower, as the bone is, so to speak, obliquely cut away, to receive the scaphoid. The proximal end is moderately convex in both directions and is not entirely covered by the radius, the ulna also resting partly upon it, which is a most unusual arrangement. Distally, the lunar covers the whole proximal end of the magnum and also extends over upon the unciform, which is likewise exceptional.

The *pyramidal* is shorter, proximo-distally, than the lunar and not quite so broad, it is of very irregular shape, so much so, in fact, that, if found isolated, one might have some difficulty in identifying it, for it has some very unusual articulations. Its greatest proximo-distal diameter is on the radial side, diminishing toward the ulnar side, or rather, end, for the dorso-palmar diameter is much contracted here. The facet for the lunar is displaced away from the dorsal and toward the palmar side. The proximal end is covered by the facet for the ulna, which is a simple, very shallow concavity in the dorso-palmar direction, almost plane transversely. The facet for the pisiform is a small, plane, quadrate surface, wider transversely than proximo-distally, it forms an angle with the facet for the ulna. The distal end of the pyramidal has a slightly saddle-shaped surface for the unciform and this continues unbrokenly into a large, moderately convex facet on the ulnar side, which articulates with the fifth metacarpal, another very unusual structural feature.

The *pisiform* is the most extraordinary bone of this extra-

ordinary carpus; it has a small plane facet for the pyramidal, but no separate one for the ulna. Though very irregular and formless, a general shape of the bone may be discerned, there is a broad head for the pyramidal, a slightly constricted neck, which expands into a wide, thick, massive and down-curved hook, but the whole is so covered with lumps and nodules of bone as to have a very pathological look. As the corresponding bone of the other side is precisely similar, it is improbable, though not impossible, that these bones are abnormal. Examples of such bilaterally symmetrical exostoses have been observed. I know of no such pisiform as this in any other mammal and it is difficult to imagine why so grotesque a shape should have been developed.

The *trapezium* is the longest bone, in the proximo-distal dimension, of the second row of carpals, and the narrowest transversely. The proximo-distal length is greatest on the dorsal side along the ulnar border and diminishes toward the palmar side, for the distal facet, which articulates with the head of the first metacarpal (mc I), is very oblique. Proximally, the trapezium has a sloping, nearly plane surface for the scaphoid and a long, narrow, flat facet for the trapezoid. Though much longer than the latter, the trapezium does not touch the second metacarpal (mc. II).

Tournouer's figure of the manus of *Parastrapotherium*¹ shows the trapezium in an altogether impossible position, which seems to indicate an opposable pollex. The two fore feet in the National Museum at Buenos Aires and the Field Museum skeleton of *Astrapotherium* show an entirely normal mode of articulation between this bone and the other carpals.

The *trapezoid* is only about two-thirds as long as the trapezium, but is much broader and heavier in every other dimension, especially in the dorso-palmar one, which is unusually great. The dorsal face is a narrow oblong, with the radial side a little longer than the ulnar, the palmar face is higher and much narrower than the dorsal and the surface is rough and irregular. The proximal facet for the scaphoid is

¹ *Soc Géol de France*, Tom IV, p 306

irregularly saddle-shaped and deeply concave palmo-dorsally, the palmar portion rising high above the dorsal; the trapezoid thus embraces the scaphoid in almost a quadrant. On the radial and ulnar sides of the trapezoid are large plane facets for the trapezium and magnum respectively. The surface for the second metacarpal is large, broad dorsally and narrowing toward the palmar side, it is rather concave palmo-dorsally, almost plane transversely.

The *magnum* is, after the *unciform*, the largest bone of the distal row and is more regularly and symmetrically shaped than the others, with nearly equal dorsal and palmar widths. The rugose dorsal face is a little shorter on the radial than on the ulnar border, toward which the proximo-dorsal edge rises, on the palmar face is the heavy, dependent, hook-like process which is usually present on this bone. The proximal surface for the lunar is slightly convex palmo-dorsally and is of nearly uniform width throughout; it is covered only by the lunar and has merely a lateral contact with the scaphoid. On the radial side of the magnum is a narrow, slightly concave facet for the trapezoid, and very obscurely demarcated from this is a small surface for the second metacarpal, while, on the ulnar side, is a large, nearly plane facet for the *unciform*. The distal surface, which rests upon the head of the third metacarpal, is somewhat warped and irregular, but is principally concave and narrows from the dorsal to the palmar side.

Ordinarily, the *unciform* is the largest bone of the carpus, but, in the present instance, it is somewhat surpassed by the lunar. This *unciform* is of extremely irregular shape, low, broad on the dorsal, narrowing to the palmar side. The proximal end is occupied by the irregularly saddle-shaped surface for the pyramidal, and on the radial side is a large flat surface for the magnum. On the distal end are three facets for the three outer metacarpals, on the radial side there is a small, oblique facet, as much lateral as distal, for the process given off from the ulnar side of the head of metacarpal III. Distally, there is the triangular, slightly concave surface for metacarpal IV and, external to that, is the convex, oblique

facet for the fifth metacarpal, which embraces the ulnar side of the unciform and extends up to a contact with the pyramidal in the manner already described.

The *Metacarpus* consists of five short, broad members, arranged in radiating fashion. In this particular individual, the first and second metacarpals are preserved for their whole length and the third has lost but little of the distal articulation, but of the fourth and fifth the distal ends have been entirely destroyed. The lacking parts may, however, be supplied from the two fore feet belonging to the Ameghino collection in the National Museum in Buenos Aires. Of these, more will be told in the sequel, as they are of some importance in the history of discovery.

In length, there is no great difference between the metacarpals, but a very considerable difference in breadth, in which dimension they increase regularly from the second to the fifth.

The *first metacarpal* (mc. I) is the shortest of the series, and has a thick and heavy proximal end, which articulates by a narrow, proximo-distally prolonged surface for the trapezium, but the bone is not connected with any other carpal or metacarpal. The position of the first digit is such that, when seen from the front, it appears to be quite slender, but, seen from the radial side, it is one of the broadest of the metacarpals. In this connection transverse width and dorso-palmar thickness become indistinguishable, and the term "broad" will be used for the shaft, which curves so as to present both laterally and dorsally. On the reverse side, chiefly palmar, the shaft is concave and the bone is so thin and plate-like that it is altogether different from the usual ungulate metapodial. No doubt some of the broadening and flattening of all the metacarpals is due to crushing, but the proportions are not very different in the Ameghino specimens, which show no sign of distortion. The radial side of the distal end has been broken away, but the trochlea would seem to have lost but little and, if so, it is very narrow, less than half the width of the shaft, and, in shape, is very low and semicylindrical. On the palmar side of the shaft, just above the trochlea, is a prominent and rugose tubercle.

The *second metacarpal* (mc II) is considerably longer and more slender than the first, the proximal end is covered by the trapezoid and there is an oblique facet which abuts against the magnum on the ulnar side of the head. The proximal end, with its two articular facets for the trapezoid and magnum respectively, has a quadrate, almost square outline, and from the palmar side is given off a broad, heavy, massive and up-curved process which projects very prominently behind. The shaft, which is somewhat narrower than the head, is considerably thicker and less plate-like than that of mc I, the trochlea is narrow and low and the tubercle on the palmar side is larger and more prominent than on mc I. The presence or absence of a carina cannot be determined for this individual, as the trochleae that are preserved are both damaged on the palmar side, where the keels should be. Ameghino's figure and my photograph of the same manus of *Parastrapotherium* were taken from the front, and if the carinae are present in this individual they are concealed from sight.

Metacarpal III is, as in *Parastrapotherium*, of approximately the same length as mc. II, but is considerably broader, the proximal end is very heavy in both dimensions, and from the palmar side arises the very prominent projection which is far larger and more massive than the similar process on mc. II. The shaft is broad and thin, though the thinness is in some degree owing to an antero-posterior compression, yet the bone, even in its original state, must have been uncommonly thin. On the proximal end are three facets, the median one of which is very much the largest and articulates with the magnum. On each side of the magnum surface is an oblique facet, a larger one on the ulnar side for the unciform, and on the radial side a smaller one for the second metacarpal. The distal end has been destroyed in both fore feet, but it is evident that not much of the length has been lost, and the Buenos Aires specimens supply the missing part.

Metacarpal IV is still broader than the third, the proximal end and palmar projection are more massive and the latter, in particular, is much broader. The only carpal with which this

bone articulates is the unciform, and on the sides of the head are small facets for the articulation with the adjoining metacarpals, mc III and V. The shaft is very broad, with concave ulnar border, widening toward the distal end; the dorsal surface is somewhat convex and the palmar side slightly concave. The very thin and plate-like shaft has suffered hardly at all from compression, at least no crushing is discernible. There appears to be some error in the assembling of the parts of the fore foot of *Parastrapotherium* figured by Ameghino, for mc IV is too slender for its position and does not make a good joint with the unciform.

Metacarpal V is the strangest of all this remarkable series, and is much the broadest of the five, and the proximal end, with its palmar projection, is much the most massive. The carpal articulations form the most peculiar feature of this highly exceptional metacarpal, for there are two well demarcated facets, one for the unciform and one for the pyramidal that projects down over the unciform, so as to reach the fifth metacarpal and form an extensive connection with it. The shaft, which has suffered little, if at all, from compression, is surprisingly broad and thin and it is difficult to imagine how such thin, plate-like metacarpals could have supported any considerable weight. As no phalanges of the manus are preserved in connection with the Field Museum skeleton, or known from any other source, it is impossible to say whether or not this was a columnar fore foot, such as elephants, hippopotamuses and very massive hoofed animals generally display, or whether it was supported by the hoofs, instead of resting upon an elastic pad.

All things considered, it seems most likely that this manus was like that of a hippopotamus, with supporting pad and nail-like hoofs. This inference is favored by the very heavy proximal ends and massive palmar projections of the metacarpals in combination with the very thin and weak distal moieties of the metacarpal shafts.

The successive steps of discovery which have brought to light the manus of the later genera of the *Astrapotheria* make

up a comedy of errors, in which everyone who has dealt with the problem has participated. A pair of fore feet from the Deseado formation, associated with no other parts of the skeleton, in the collection of Sr. Ameghino, were by him referred to *Pyrotherium* and so described. M. Tournouer, who had collected in Patagonia for the Paris Museum, argued that Ameghino's specimen was properly assignable to *Astrapotherium* (i. e. *Parastrapotherium*) and published, with Gaudry's approval, a figure of his own, in which the trapezium was given an impossible position, but which made it very probable that Ameghino's figures were not properly referable to the *Pyrotheria*. Professor Loomis was of the opinion, which he subsequently retracted, that Ameghino was right in referring these feet to *Pyrotherium*, Tournouer and Gaudry wrong in assigning them to the *Astrapotheria*. In my report on the Santa Cruz members of this group, I presented a figure made up from my photograph of Ameghino's specimen and Tournouer's drawing and referred it, though with grave doubt, to *Parastrapotherium*. My contribution to the series of errors was to give an entirely incorrect drawing of the first metacarpal.

Mr. Riggs' discovery of the skeleton of *Astrapotherium magnum* in the Santa Cruz beds, which is now in the Field Museum, and with which all four feet are associated in their original connections, removes all doubt as to the essential correctness of Tournouer's determination, although his figure is, in some respects, inaccurate. The gait in general, and the attitude of the fore feet, in particular, can most conveniently be dealt with in connection with the hind feet.

The Pes. Anyone who has looked through the foregoing osteological description will be prepared to agree that the *Astrapotheria* comprise some of the strangest and most grotesque mammals of which we have any knowledge. Of all the curious features which are associated in this bizarre skeleton, none other is so inexplicable as the hind foot, every part of which is exceptional, often unexampled and unique. (Pl. V, Fig. 1.)

The *astragalus*, in its general appearance and proportions, bears considerable resemblance to that of the Amblypoda, of the North American Eocene, as was long ago pointed out by Schlosser. The trochlea for articulation with the tibia is very nearly flat, but slightly concave transversely and rising considerably toward the fibular side, the tibial side is emarginated by a large, deep fossa, into which fits the internal malleolus of the tibia. This process, as was noted above, has an articular surface on the distal end. The external side of the astragalus is taken up by the large surface for the fibula, which is gently convex. There is no neck and the broad, thick, convex head fits into the deeply concave proximal side of the navicular and does not touch the cuboid. On the plantar side are two large facets for the calcaneum, the dorsal face of which is entirely covered by the astragalus. The external calcaneal facet is very large and of nearly square outline, with rounded angles, and is slightly concave. The sustentacular surface, which is separated from the external calcaneal facet by a deep sulcus, is placed at a more distal level on a heavy mass which is formed by the astragalar head. Thus, when the astragalus is viewed from the distal end, it looks somewhat like an artiodactyl cuboid. The facet for the sustentaculum is thus directly plantar to the head of the astragalus, an arrangement which is occasioned by the absence of any neck. The facet itself is broad distally, narrowing proximally and again expanding, where it curves down behind the sustentaculum. The curiously shaped facet is thus in two parts, a broader distal and narrower proximal portion, connected by a narrow band, where a large sulcus invades it from the tibial side, dorsally, this same sulcus bounds the fossa for the internal malleolus of the tibia, and separates it from a heavy proximal projection. On the dorsal side, this projection carries a tongue of the trochlea and, on the plantar side, the proximal part of the facet for the sustentaculum.

Altogether, this astragalus, despite its general likeness to that of *Uintatherium*, is one of the most peculiar ankle-bones ever discovered and it is exceedingly difficult to give any proper notion of it by description.

That the astragalus of the Santa Cruz genus bears some resemblance to that of the North American *Amblypoda* has been noted by all observers since Schlosser first pointed it out, but the likeness is superficial and extends only to the general outline and the character of the tibial trochlea, features which are as much Proboscidean as Amblypodan. *Uintatherium* has no articular pit, internal to the trochlea, for the reception of the internal malleolus of the tibia and the plantar side and distal end of the astragalus are altogether different from those seen in *Astrapotherium*. In the North American animal the astragalus has a neck, though an extremely short one, which prevents the navicular surface from reaching and forming an angulation with the trochlea. The astragalar facets for the calcaneum are as unlike as possible in the two groups, in size, shape and position. None of the characteristic peculiarities of the astragalus of *Astrapotherium* is repeated in *Uintatherium* and no other bone of the skeleton displays so much resemblance between the North and South American genera as does the astragalus.

In the Chicago skeleton the *calcaneum* has, in both hind feet, been somewhat damaged by crushing and by weathering, but it has not been greatly injured and, happily, suffices to put beyond all doubt the fine, perfectly preserved specimen in the Ameghino collection, which I figured in my account of the order in the Patagonian Reports (Vol. VI, p 330, Pl XXXVII, Fig 3). This bone, though found isolated and completely uncrushed, undistorted and not in the least injured by weathering, was, through a process of elimination, identified by Ameghino as belonging to *Astrapotherium* and the reference is confirmed by the Field Museum skeleton, as above mentioned. The Ameghino specimen is considerably larger than the calcaneum of the Chicago individual and may have belonged to a different species, but there is no way of determining this.

The calcaneum is even more peculiar than the astragalus and is entirely unlike that of any other known ungulate. The astragalus extends over the whole width of the calcaneum,

excluding the latter from the fibula. In all the other ungulate groups of the Santa Cruz formation, Toxodonta, Typotheria, Entelonychia, and Litopterna, the calcaneum has a large facet upon which the fibula rests. *Astrapotherium* thus differs from all the other groups, but, whether this difference has arisen in the course of Tertiary time, or, whether from the beginning of their history as an order, the Astrapotheria have been without the calcaneo-fibular articulation, cannot be determined, until the foot-structure of such Casa Mayor genera as *Albertogaudrya* shall have been brought to light.

On this calcaneum, the external astragalar facet is very large and especially elongate proximo-distally, relatively rather narrow transversely and convex in both directions. Between this outer facet for the astragalus and the sustentaculum is a very deep fossa, of irregularly conical shape, which almost perforates the bone. The sustentaculum is large, prominent and very thick, seen from the dorsal side, it has a nearly quadrate outline and the astragalar surface consists of two concavities, proximal and distal, which form a continuous articular surface that is also reflected over upon the proximal border of the sustentaculum. The distal border of the same process also bears a narrow articular band, which can only be for the navicular. I cannot confirm this inference, however, from the Field Museum skeleton, for, both on the calcaneum and the navicular, these bones are so eroded as to destroy the articular surfaces. The facet for the cuboid is extremely peculiar and unlike any other with which I have been able to compare it, it is notably small, covers but little of the distal end of the calcaneum, and presents inwardly (*i.e.* toward the tibial side) as much as distally. That part of the calcaneum which is distal to the sustentaculum is very short and, on the plantar side, is extremely massive. On the fibular side is a prominent and heavy process, which, presumably, served for ligamentous attachment. The *tuber calcis* is short and very massive.

No other Santa Cruz mammal has a calcaneum which, even remotely, resembles this. The absence of any articulation

with the fibula, the shape and position of the cuboid facet, the form of the sustentaculum and the distal external process are all unique features.

If there is some superficial likeness in the astragalus between *Astrapotherium* and the Amblypoda, there is none whatever in the calcaneum. In *Uintatherium* the calcaneum has an extremely short, thick tuber and a relatively enormous sustentaculum, which is nearly as large as all the rest of the bone, and its articular surface is convex and larger than the external astragalar facet. There is a small surface for the fibula, at least in some individuals, while in the more ancient *Coryphodon*, of the same ordinal group, the fibular facet is very large. No two large and heavy calcanea could be less alike than these.

No element of this extraordinary foot is more peculiar than the *navicular*, which is very broad and of excessively small proximo-distal diameter, the ratio of width to length being 6.5 to 1. The whole bone is curved and looks like a small slab of clay or wax that had been moulded around the convex head of the astragalus, rising much higher toward the fibular side. The proximal surface into which fits the head of the astragalus is deeply concave transversely, planto-dorsally it is but slightly curved. On the distal side of the navicular are facets for the three cuneiforms.

This skeleton makes it evident that the isolated navicular in the Ameghino collection, which I figured¹ as referable to the present genus, was incorrectly identified.

The surface for the entocuneiform is the largest of the distal facets and is also very oblique and convex, it occupies the tibial side of the internal, upcurved portion of the navicular. This surface for the entocuneiform is broad on the dorsal, narrowing toward the plantar side. In direction, the facets for the first and third cuneiforms make almost a right angle. The surface for the mesocuneiform is transverse and convex, while that for the ectocuneiform is narrow, but greatly extended in the dorso-plantar dimension.

¹ Reports Princeton University Exped. to Patagonia, Vol. VI, Pl. XXXVII, Figs 4 and 4a.

The *entocuneiform* is, as the surface for it on the distal side of the navicular shows, the largest of the series, the principal diameter is the dorso-plantar one, but, in width and in proximo-distal length also, it exceeds either of the other cuneiforms. The proximal facet for the navicular is large, of irregularly kidney-shaped outline and is a warped surface. The distal facet for the head of the first metatarsal (mt I) is deep planto-dorsally, narrow, oblique and concave.

The *mesocuneiform* is much damaged, but it may be seen that the dorsal surface is exceedingly small and that the bone is narrow transversely, but much extended planto-dorsally.

The *ectocuneiform* is an extraordinary bone, its dorso-plantar diameter being out of all proportion to the proximo-distal one, in the ratio 17 : 6, the small, almost square, dorsal face gives no idea of the great planto-dorsal depth. The bone narrows somewhat toward the plantar side, near which it curves slightly to the tibial side. The proximal surface for the navicular is simply concave planto-dorsally, as is the distal facet for the head of the third metatarsal (mt. III), but that surface is slightly warped.

The *cuboid* is, as is normally the case, the largest bone in the distal row of tarsals, but like all the rest of these elements, it is extremely peculiar, it is short proximo-distally, of moderate transverse width and great dorso-plantar thickness, toward the plantar face, the bone narrows much and on that side is a rugose prominence, which projects out behind the articular surfaces. The facet for the calcaneum is small. On the distal end are the facets for the fourth and fifth metatarsals (mt IV and V) but they are made indistinguishable by the slight amount of erosion which has roughened the articular surfaces.

The *Metatarsus*, like all other parts of the skeleton, is extremely peculiar, more so than most of the other structures, and the relative sizes of its members are different from those displayed in any other mammal with which I am acquainted. Indeed, it is probable that were this pes more complete, and the phalanges and distal ends of the metatarsals preserved, it

would seem even more exceptional than it does in its present condition. The fourth and fifth members of the series (mt. IV and V) are nearly of their original length and the third (mt III) has lost but little, but the second (mt II), and more particularly the first (mt. I) are of indeterminable lengths.

Metatarsal I is entirely undistorted and uncrushed, but may have lost as much as half its original length. The proximal end is relatively heavy, both broad and thick, but has only a short projection from the plantar side, the facet for the entocuneiform is a large saddle-shaped surface. The shaft is broad, broader than that of any other metatarsal, except mt V, but very thin and plate-like, slightly convex transversely on the dorsal side, more decidedly concave on the plantar

The *second and third metatarsals* (mt. II and III) are much the most slender of the series and have such a withered, atrophied look, as strongly to suggest that they are abnormal and pathological in character. This suggestion is, however, rendered improbable by the fact that in both right and left feet these metatarsals are of precisely similar character and it must be assumed that these bones are normal. Mt II has an injured proximal end and had lost the large process on the plantar side which the three outer metatarsals (mt III, IV and V) display, but the great dorso-plantar diameter of the mesocuneiform indicates the form and presence of this process on mt II also. The shaft may be described as very short, for, though the trochlea has been broken away, yet the beginning of the distal expansion remains and that gives approximately the length of the shaft. The dorsal face of the shaft has been crushed in and seamed in longitudinal cracks, a condition which adds much to the withered and diseased look of this and, in less degree, of the third metatarsal, but the plantar side is uninjured. As in all the metapodials, the shaft is thin planto-dorsally in proportion to its transverse width, yet very narrow and slender as compared with the other metatarsals, except mt III, which is even more slender. The tibial border of the shaft is concave, the fibular border straight.

Metatarsal III is also greatly reduced in size and, like mt. II, seems to be in process of atrophy; it is short and probably but little longer than the entire mt II would be, if preserved. The proximal end is relatively heavy, having a great posterior prolongation or plantar process. The shaft is slender, with concave tibial and nearly straight fibular border, thick at the proximal end, but rapidly thinning distally. The distal expansion is relatively broad, narrowing to the trochlea, which is lost, apparently by corrosion or abrasion, so that very little of the total length has been removed. Mt. II and III form a pair conspicuous for their small size and they seem to be quite out of place in this foot. It remains to be determined whether these bones are normal, or pathological.

Metatarsal IV is decidedly larger in every dimension than mt III except in length, which does not greatly exceed that of mt III, but it is broader and thicker and in every way stouter. The head is rather broad and is made very thick planto-dorsally by the plantar projection, which, however, does not carry an extension of the tarsal articular surface, as it does in mt. III and, presumably, also in mt II. The shaft is narrower than that of mt I or V, broader than that of mt. II or III, and widens very gradually toward the distal end. The proximal portion of the shaft is thick planto-dorsally, but thins rapidly downward, making the distal third plate-like. Little can be said of the trochlea, which has suffered from erosion, but evidently it was very low and appears to have had a vestige of the carina.

Metatarsal V is the strangest element in all this paradoxical foot and rather resembles the calcaneum of a Santa Cruz ground-sloth than the actual metapodial of an ungulate, which it unquestionably is. The proximal end is about as wide as that of mt IV and bears two facets, one of these is proximal in position and is moderately convex, fitting into the shallow concavity of the cuboid, the other is oblique and articulates with the head of mt. IV. When these two metatarsals are fitted together by their articular surfaces, it is seen that mt V diverges from mt. IV at an acute angle, though

all the digits have a spreading arrangement. The plantar projection from the head of mt. V is broader than in any of the other metatarsals, as well as more massive and rugose, but is not nearly so long and prominent, and is confined to the fibular side of the plantar surface.

The shaft expands suddenly from the head and becomes much broader than in any other metatarsal, the tibial border is nearly straight, but the fibular border is convexly curved, gently narrowing the shaft toward the distal end. The shaft is very thin planto-dorsally, the dorsal face is convex, while the plantar is deeply sulcate by a fossa that will hold the tip of the little finger. No trochlea remains and it seems doubtful whether there ever could have been a trochlea, or what sort of a phalanx could have been attached to it. In short, this bone is as unlike a normal ungulate metatarsal as it could well be.

Phalanges—Two phalanges, the first and second of the same digit, occur in connection with one of the hind feet, though because of the lack of well-preserved trochleae to which they might be fitted, it is difficult to determine the digit to which they may have belonged. Assuming that these phalanges are actually referable to *Astrapotherium* (and the only reason for doubting that reference is their incongruous character), they are the most surprising and unexpected feature of a most paradoxical skeleton. Instead of the broad, heavy and block-like phalanges, more or less elephant-like in character, which one would expect to find in connection with such metapodials, we find long, slender, and delicate bones, not unlike those of the Tertiary three-toed horses.

The *first phalanx* has a relatively broad and thick proximal end, on which the surface for the metatarsal is a simple, transverse concavity, without groove or notch for a carina. The body, or shaft, of the phalanx is somewhat narrower and very thin, while the distal end is again thickened, though not so much so as the proximal end. The distal surface for the second phalanx is semi-cylindrical, made very slightly hour-glass shaped by a median depression.

The *second phalanx* is much like the first, though on a smaller scale, it is unusually long in proportion to the first. It is broadest and thickest at the proximal end, where the articular surface for the first phalanx is very obscurely divided into two concavities, and a median dorsal beak is faintly indicated. The shaft narrows to a waist and then broadens slightly to the distal end, which is considerably narrower than that of the first phalanx. The distal trochlea is semicylindrical, but is reflected somewhat further upon the dorsal side than in the first phalanx. On the fibular part of the trochlea is a curious little convexity, the meaning of which, in the absence of the ungual, is not obvious.

As is the rule among the larger Santa Cruz ungulates, the feet of *Astrapotherium* are very small in comparison with the size of the body and length of the limbs, the metapodials in particular are relatively very short. How these extraordinary feet were used and what sort of gait the animal had are very puzzling questions, the difficulty of which is increased by the lack of any phalanges of the fore feet. The relations of the carpus to the forearm bones would seem to imply a digitigrade position for the manus, but the thin, flat metacarpals must have been incapable of carrying their share of the body-weight, unless they were supported by a large elastic pad, as in the elephants. In the drawing of the skeleton the fore feet are represented in digitigrade position, though, at any time, the discovery of phalanges, especially of unguals, may necessitate a change to a plantigrade, or semi-plantigrade attitude.

The problem of the hind foot is different and is rendered even more obscure by the discovery of phalanges which seem so incongruous and incompatible with the rest of the pes. I was much interested to observe that Mr. Riggs and Mr. Gronemann had, without any suggestion from me, drawn the skeleton with digitigrade fore feet and plantigrade hind feet, and, tentatively at least, I must accept their conclusion. So far as the hind feet are concerned, no other gait seems possible, for, when the astragalus and tibia are fitted together, there

is very little freedom of motion at the ankle-joint and the plantigrade position seems to be the only one the skeleton of the foot is capable of taking. If it be objected that, in hoofed animals, such a difference in the attitude of fore and hind feet is unprecedented and highly improbable, it may be replied that in *Homalodotherium*, also of the Santa Cruz formation, there is every appearance of an even greater difference. A difference, similar in kind, though less in degree, may be observed in the Lower Eocene *Coryphodon*, of the northern hemisphere.

It must be remembered that, outside of its own order, no mammal, fossil or Recent, in the least like *Astrapotherium* is anywhere known. A few points of resemblance to one form or another may be observed, such as the scapula of *Coryphodon*, but such isolated likenesses have little significance, as a whole the skeleton of *Astrapotherium* is unique, and therefore it is a law unto itself, not bound by precedents. Needless to say, these observations do not refer to the fundamental characteristics of mammals in general, or of ungulates in particular.

The problems of the feet are by no means all concerned with those of gait and attitude. What can be the meaning of the partial, or incipient, atrophy of the second and third digits of the hind foot? Disease immediately suggests itself, but is rendered improbable by the exactly similar condition of both right and left feet. The phalanges, too, increase the difficulty of understanding these feet, for they are altogether unlike what might have been inferred from the character of the metapodials; one can hardly imagine what a foot, made up of such metatarsals and such phalanges, can have been like in the living animal, whatever its gait may have been.

There is another characteristic of the pes which it is exceedingly difficult to understand and interpret, viz., the extreme dorso-plantar thickness of the distal row of tarsal bones and of the proximal moiety of the metatarsals, combined with the extraordinary, plate-like thinness of the distal half of the metatarsals. What can be the meaning of this excep-

tional thickness in one part of the foot, changing to an equally exceptional thinness in another part, and how could such a foot have been used? The shape of the external metatarsal (mt. V) suggests that, in walking, the hind foot rested upon the fibular border, turning the sole inward, as in one of the ground-sloths, but the tarsal and tarso-metatarsal articulations appear to show that this cannot have been the case. As to the entelonychian *Homalodotherium*, also of the Santa Cruz, there is strong reason to believe that that grotesque creature walked upon the fibular edge of the hind foot, as was first suggested by Ameghino, for in *Homalodotherium* the astragalus has a long neck and hemispherical head, which had such freedom of rotation upon the navicular as to allow the pes to turn through an arc of more than 90°. In *Astrapotherium*, on the other hand, the movements of the tibia on the astragalus and of the astragalus on the navicular were very limited and, according to all appearances, it would be quite impossible to bring the outer border of the foot to the ground. The unfortunate loss of the phalanges, and especially of the unguals, gives additional obscurity to these and other problems.

Almost every part of the skeleton presents its own difficulties in the way of an understanding of the habits and mode of life of this paradoxical creature. One of the outstanding problems concerns the head and how to interpret the extreme reduction of the premaxillaries and nasals and the backward displacement of the anterior narial opening. The nasal canal passes almost vertically through the head, nearly as much so as in the elephants, and the reduction of the nasal bones is but little less extreme than in the Proboscidea. In terrestrial mammals such reduction of the nasals and such a position of the nasal canal almost always indicate a proboscis of some kind, either long, as in the elephants, or short, as in the tapirs. The *Astrapotherium* skull immediately suggests the presence of a proboscis, and when Mr. Horsfall was making his restoration of the head for my *History of Land Mammals in the Western Hemisphere* (Fig. 254, p. 510) I advised the addition

of a short trunk On first seeing the Field Museum skeleton I was immediately struck by the length of the neck, which, in addition to that of the head and in association with the short legs and feet, seemed to render a proboscis unnecessary.

The Saiga Antelope (*Saiga tatarica*) next suggested itself as offering an explanation of the *Astrapotherium* skull, for in that Recent animal the shape and position of the anterior nasal opening are very much as in the Santa Cruz fossil, and the inflated snout takes the place of a proboscis. There is, however, a significant difference between the two skulls, in the Saiga the maxillaries and premaxillaries are unreduced in length and the premaxillae support the elastic pad against which the lower incisors bite in grazing In the Santa Cruz genus, on the contrary, the premaxillae are mere vestigial lumps and do not extend nearly so far forward as the lower incisors, which, seemingly, had nothing against which they could bite. All the bony structures of the skull are far behind the line of these teeth, which, nevertheless, were obviously in habitual use, as is demonstrated by the manner in which they are always abraded in old animals, where they are worn to stumps

All things considered, it seems to me that the proboscis still offers the best solution of the contradictory difficulty. An analogous condition is presented by the Miocene and Pliocene Proboscidea, which had functionally important lower tusks, that give every evidence of abrasion by the trunk If we imagine that *Astrapotherium* possessed a short proboscis, upon the under side of which was a thick dermal, or horny pad, against which the lower incisors impinged, there would be provided a structure which seems best to meet the requirements of the skull and lower jaw.

Another set of unintelligible structures is met with in the vertebral column, which were pointed out in the description of the backbone, but may be summarized here in connection with the paradoxical features of the skull, feet and limbs. (1) There is the extraordinary size of the cervical vertebrae in comparison with those of the dorsal and lumbar regions.

This same disproportion between neck- and trunk-vertebrae is observable in the more ancient *Parastrapotherium* of the Colhué-huapi and Deseado stages, but of the still earlier *Astraponotus* of the Musters, and *Albertogaudrya* of the Casa Mayor, no vertebrae are known, and therefore it cannot yet be stated at what point in the line of descent this peculiar feature appeared

(2) Still another remarkable characteristic of this skeleton, which is very difficult of explanation, is to be seen in the very short and weak neural spines of all the vertebrae. With the massive head and heavy neck, one would expect to find very long neural spines in the anterior dorsal region, such as are to be seen in the contemporary toxodont, *Nesodon*, for attachment of the large muscles and ligaments which supported the head. Such long spines in the withers are very general in the large and massive hoofed animals, such as elephants, bison, rhinoceroses and, pre-eminently, in the extinct titanotheres and toxodonts, in which the anterior dorsal spines reach extraordinary proportions, and must have made a prominent hump at the shoulders.

(3) In the lumbar region the neural spines are of ordinary length and thickness, but the transverse processes are singularly short, slender and weak. In the lumbar and posterior part of the dorsal region the zygapophyses have attained an unusual degree of complexity, developing a scroll-like cross-section elsewhere found only in the entelodonts, or "giant pigs," of the Oligocene and Miocene of the Northern Hemisphere. Why such an uncommon degree of combined strength and flexibility should have been needed in these relatively weak vertebrae, it is difficult to imagine

(4) Finally, as concluding the list of peculiarities in the vertebral column of *Astrapotherium*, should be mentioned the sacro-iliac articulation, in which the sacrum is attached to the pelvis, for its whole length of five vertebrae and ankylosed with it, another instance of unusual strength. §

The skeleton as drawn by Gronemann does not seem at all unusual until the details are examined. The general pro-

portions of head, neck, trunk and limbs are not far from those of the North American amblypods, *Uintatherium* and *Coryphodon*, especially the latter, because of the shorter limbs. It is when the minor details are studied that the mass of paradoxes and self-contradictions are brought to light. No animal in the least resembling *Astrapotherium* is alive to-day, and, outside the genera of its own order, none in the least like it has been found among the fossils. It is this extreme degree of isolation which makes the interpretation of the structural peculiarities so difficult. Perhaps the suggestion that this strange beast was amphibious in mode of life would best account for these peculiarities, although this and all other attempts at explanation that have so far been made encounter difficulties and objections at every turn. The hypothesis of amphibious habits receives some support from the fact, of which Mr Riggs tells me, that, in both the Santa Cruz and Deseado formations, the bones of *Astrapotherium* and *Parastrapotherium* are commonly found in and near the ancient stream-channels. Such an association is, of course, not decisive, but it is not without significance, as appears from the analogous case of *Metamynodon*, a rhinoceros, believed to be aquatic, from the Oligocene of North America and Mongolia. The very frequent association of the bones of this animal with the cross-bedded "channel sandstones" of the White River Bad Lands, has been regarded as a confirmation of the inference drawn from skeletal structure that this rhinoceros was amphibious in habits.

A comparison of the skeleton of *Astrapotherium* with that of *Hippopotamus* is not favorable to the aquatic hypothesis for the former, for there is hardly any likeness between them, the short massive limbs and sturdy foot-bones of the modern genus being very different from the relatively slender legs and small, weak feet of the fossil. This comparison is, however, not at all decisive, for among existing aquatic mammals there are great differences in the skeleton, according to size and body-weight. *Astrapotherium* had no such colossal weight of head and body to support as has *Hippopotamus*,

for the visceral cavities were far less capacious. Even the enormous *Parastrapotherium*, of the Deseado, the skeleton of which is still incompletely known, did not have the *relative* massiveness of the modern animal.

Short of the development of flippers, there seems to be no general character of skeleton which distinguishes aquatic from terrestrial mammals. In some instances, the skull does display such characters, but by no means always. In the skull of the Hippopotamus, for example, the orbits and the entrances to the ears have a very elevated position and, in life, the nostrils open upward. The animal can thus lie afloat, with only ears, eyes and nostrils above the water-level and these, at a little distance, are almost invisible. Among the fossils, the oreodont, *Leptauchenia*, had a similarly elevated orbit and auditory entrance (the position of the nostrils is not indicated by the bones) and in *Metamynodon* the orbits project above the level of the forehead, as in *Hippopotamus*, but there are other aquatic mammals, such as otters, muskrats, beavers and the Capybara (*Hydrochoerus*), in which the skull displays no distinctively aquatic characteristics.

The skull of *Astrapotherium* has no such characters and the position of the orbits is conspicuously low on the sides of the face. The hypothesis of an amphibious mode of life is thus very uncertain, but, nevertheless, it seems to be the most likely explanation of the extraordinary characteristics of this unique skeleton.

P S It is impossible not to speculate concerning the habits and appearance in life of this strange and paradoxical animal, the structural characteristics of which are often so incongruous and contradictory. A great obstacle in the way of interpreting these characteristics is the lack of any living animal which, even remotely, resembles *Astrapotherium*. The fore feet are more or less proboscidean, or amblypodan in general aspect, but the hind feet are almost as strange, in their own way, as those of the great marsupial *Diprotodon* of the Australian Pliocene. Both fore and hind feet agree, however, in one very exceptional if not unique characteristic, viz., the

sudden and abrupt change in dorso-plantar thickness of the metapodials, distally to which these bones are remarkably thin and plate-like. This sudden reduction in thickness must indicate a change at those points in the nature and direction of the stresses due to body-weight and the movements in walking or running. The suggestion commends itself that, at those points, a pad assumed the weight and that the bones became, mechanically, relatively unimportant. Although fore and hind feet appear to be strongly contrasted in attitude and gait, the fore feet digitigrade and the hind feet plantigrade, that is no objection to the inference that, in both, the weight was chiefly borne upon pads, in one case behind the metapodials, and in the other, below them. Confirmation, or disproof, of this hypothesis will probably be determined by the discovery of representative phalanges and, more especially, of unguals.

All the measurements in the subjoined table are taken, unless it is otherwise stated, from the skeleton in the Field Museum (No. P 14,251)

MEASUREMENTS

	mm
Skull, length, occ cond to prmx, incl	590
Mandible, length, angle to incisors, incl	483
Mandible, height at condyle	230
Mandible, height at coronoid	298
Atlas, length, ant.-post	167
Atlas, width over trans proc	236
Atlas, neural canal, dorso-vent diam	92
Atlas, neural canal, transverse diam	67
Atlas, transv proc, width from post cotyl	49
Axis, length from odontoid	192
Axis, length from anterior cotyles	122
Axis, ant.-post diam of neur spine on dors border	135
Axis, width of centrum over cotyles	150
Axis, width of centrum, post face	75
Axis, width over post-zygapophyses	95
Third Cervical, length of centrum	93
Third Cervical, length over zygapophyses	116
Third Cervical, width of anterior face	45
Third Cervical, width over post-zygapophyses	103

N B All the vertebrae of the neck, save the atlas, have been left in connection with one another and the convex anterior faces of the centra are slightly hidden, but the figures given in the table above are close approximations

MEASUREMENTS (Cont.)

	mm
Fourth Cervical, length of centrum (approx)	96
Fourth Cervical, length over zygapophyses	112
Fourth Cervical, width of anterior face	45
Fourth Cervical, width over prezygapophyses	106
Fifth Cervical, length of centrum (approx)	90
Fifth Cervical, length over zygapophyses	114
Fifth Cervical, width of anterior face	48
Fifth Cervical, width over prezygapophyses	106
Sixth Cervical, length of centrum (approx)	89
Sixth Cervical, length over zygapophyses	114
Sixth Cervical, width of anterior face	54
Sixth Cervical, width over post-zygapophyses	109
Seventh Cervical, length of centrum (approx)	65
Seventh Cervical, length over zygapophyses	87
Seventh Cervical, width of anterior face	54
Seventh Cervical, width over post-zygapophyses	124
First Dorsal, length of centrum	44
First Dorsal, length over zygapophyses	80
First Dorsal, width over prezygapophyses	150
Third Dorsal, length of spine from centrum	127
Sixth Dorsal, length of spine from centrum	85
First Lumbar, width of spine at end	47
Second Lumbar, width of spine at end	52
Third Lumbar, width of spine at end	58
Fifth Lumbar, width of spine at end	37
Sacrum, length of sacro-iliac joint	255
Sacrum, width between ilia	187
Scapula, vertical length to glenoid cavity	465
Scapula, vertical length to tip of acromion	510
Scapula, greatest width	215
Scapula, ant -post diameter of glenoid cavity	114
Scapula, transverse diameter of glenoid cavity	70
Scapula, width of acromion	126
Humerus, length from head	490
Humerus, length from ext. tuberosity	523
Humerus, greatest thickness of shaft	91
Humerus, ant -post diameter of head	99
Humerus, transverse diameter of head	91
Humerus, width of trochlea	84
Radius, length	348
Radius, width of proximal end	81
Radius, thickness of proximal end	58
Radius, width of distal end	65
Radius, thickness of distal end	59
Radius, median width of shaft	49
Radius, median thickness of shaft	31
Ulna, length from olecranon	460
Ulna, length from coronoid process	410
Ulna, length from ext. humeral surface	339
Ulna, width over humeral facets	87
Ulna, median width of shaft	46
Ulna, median thickness of shaft	51
Ulna, width of distal end	39

MEASUREMENTS (Cont)

	mm
Ulna, thickness of distal end	61
Carpus, width, proximal row	112
Carpus, prox-distal length, median	75
Pisiform, length	52
Pisiform, proximal width	26
Pisiform, distal width	28
Pisiform, distal thickness	38
Metacarpal I, length	62
Metacarpal I, width of proximal end	22
Metacarpal I, thickness of proximal end	43
Metacarpal I, width of shaft	20
Metacarpal I, thickness of shaft	33
Metacarpal II, length	84
Metacarpal II, width of proximal end	33
Metacarpal II, thickness of proximal end	47
Metacarpal II, width of shaft	23
Metacarpal II, thickness of shaft	18
Metacarpal III, length	75
Metacarpal III, width of proximal end	37
Metacarpal III, thickness of proximal end	49
Metacarpal III, width of shaft	30
Metacarpal III, thickness of shaft	14
Metacarpal IV, width of proximal end	40
Metacarpal IV, thickness of proximal end	51
Metacarpal IV, width of shaft	38
Metacarpal IV, thickness of shaft	14
Metacarpal V, width of proximal end	50
Metacarpal V, thickness of proximal end	45
Metacarpal V, width of shaft	44
Metacarpal V, thickness of shaft	9
Ilium, length	340
Ilium, width of plate	240
Femur, length from head	570
Femur, length from great trochanter	530
Femur, proximal width	142
Femur, thickness of great trochanter	51
Femur, median width of shaft	66
Femur, median thickness of shaft	39
Femur, width of distal end, above condyles	118
Femur, thickness of distal end	104
Femur, width of rotular groove	52
Tibia, length (internal)	399
Tibia, length (external)	383
Tibia, width of proximal end	90
Tibia, width of distal end	78
Tibia, thickness of distal end	43
Fibula, length	372
Fibula, width of proximal end	17
Fibula, thickness of proximal end	30
Fibula, median width of shaft	21
Fibula, median thickness of shaft	22
Fibula, width of distal end	78
Fibula, thickness of distal end	43

MEASUREMENTS (Cont.)

	mm
Fibula, thickness of distal end	43
Patella, length	109
Patella, width	51
Patella, thickness	35
Astragalus, proximo-distal length	73
Astragalus, width	66
Astragalus, thickness at ext. calc. facet	56
Astragalus, thickness at sustentac. facet	42
Navicular, proximo-distal length	10
Navicular, width	65
Navicular, dorso-plantar thickness	49
Entocuneiform, proximo-distal length	25
Entocuneiform, width	17
Entocuneiform, dorso-plantar thickness	31
Ectocuneiform, proximo-distal length	31
Ectocuneiform, dorsal width	17
Ectocuneiform, dorso-plantar thickness	52
Cuboid, max. length, dorsal face	22
Cuboid, dorsal width at distal end	36
Cuboid, dorso-plantar thickness	52
Metatarsal I, proximal width	31
Metatarsal I, proximal thickness	29
Metatarsal I, width of shaft	26
Metatarsal I, thickness of shaft	12
Metatarsal II, proximal width	22
Metatarsal II, mid-shaft, width	15
Metatarsal II, mid-shaft, thickness	10
Metatarsal III, proximal width	15
Metatarsal III, proximal thickness	39
Metatarsal III, mid-shaft, width	12
Metatarsal III, mid-shaft, thickness	11
Metatarsal III, approximate length	71
Metatarsal IV, proximal width	28
Metatarsal IV, proximal thickness	43
Metatarsal IV, mid-shaft, width	22
Metatarsal IV, mid-shaft, thickness	13
Metatarsal IV, approximate length	78
Metatarsal V, proximal width	29
Metatarsal V, proximal thickness	30
Metatarsal V, greatest width of shaft	39
Metatarsal V, mid-shaft, thickness	11
Metatarsal V, approximate length	70
First Phalanx, length in median line	32
First Phalanx, proximal width	20
First Phalanx, proximal thickness	14
First Phalanx, distal width	16
First Phalanx, distal thickness	10
Second Phalanx, length	26
Second Phalanx, proximal width	18
Second Phalanx, proximal thickness	10
Second Phalanx, distal width	13
Second Phalanx, distal thickness	8

PARASTRAPOTHERIUM Ameghino

Parastrapotherium Amegh.: *Bol. Inst. Geogr. Argentino*, T. XVI, p. 635.

Astrapotherium Gaudry (*nec* Burmeister), *Ann. de Paléont.*, T. I, p. 29.

Typically, this is a *Deseado* genus, but its upward range is still unknown, for its distinctive characters are found in the teeth and in the Field and American Museums are several individuals from the Colhué-huapi and Santa Cruz stages with which no teeth are associated and the generic reference of which is therefore uncertain. Both genera apparently occur in the Colhué-huapi together with a third, which is nearly, or quite, confined to that stage, the *Astrapothericulus* of Ameghino. Species of the *Deseado* genus are, generally speaking, larger than those of the Santa Cruz, but the *A. giganteum*, of the latter stage, is as large as the *Deseado* individuals of *Parastrapotherium*, to which, indeed, that species may be referable. Ameghino's descriptions of several supposed species of *Astrapotherium* leave it entirely doubtful, as he himself points out, whether the generic identification is correctly made. *A. herculeum*, which he calls "vraiment colossale," is generically indeterminable. He says "Les matériaux pour le moment à ma disposition ne me permettent pas de décider si cette espèce est un vrai *Astrapotherium*, ou un *Parastrapotherium*" (*Bol. Acad. Nac. de Cienc. de Córdoba*, T. XVII, p. 93).

Ameghino's original description of *Parastrapotherium*, founded upon very imperfect material, was largely made up of inferences, which, for the most part, subsequent discovery has shown to be mistaken. Nevertheless, he had the correct instinct that the two genera were different. "Ce genre se distingue facilement d'*Astrapotherium* par le nombre plus considérable des prémolaires supérieures et inférieures, ces dents étaient probablement en nombre complet. Les incisives inférieures sont beaucoup plus fortes et il est probable qu'il eût aussi des incisives supérieures" (*Bol. Inst. Geograf. Argent.*, T. XV, cahiers 11 and 12, separate p. 35). As a

matter of fact, the dental formula differs from that of *Astrapotherium* only in the presence of an additional premolar above and below. The premaxillae are not known, but, from the attachments for them on the maxillaries, there is every reason to infer that they were essentially similar to those of *Astrapotherium* and were therefore edentulous. The generic distinction rests upon the greater number of premolars and upon differences in the molar structure, above and below, which are slight, but significant.

Before taking up the systematic description it will be useful to enumerate the specimens upon which it is founded, the Field Museum possesses the following material

PARASTRAPOTHERIUM

Skull, palate and base of cranium, with all the upper teeth (No P13,329)	Deseado
Upper jaw, with p4-m2 (No. P13,504)	Deseado
Mandible, both rami and all teeth except incisors and p3 (No P13,365)	Deseado
Mandible, fragment, with m1 and m2 (No P13,369)	Deseado
Mandible, fragment, with p4-m3 (No P13,492)	Deseado
Mandible, fragment, with p3 and p4 (No P15,067)	Deseado
Mandible, fragment, with m2 and m3 (No P13,473)	Deseado
Mandible, fragment, with m3 (No P13,347)	Deseado
Mandible, jaw, with all milk-teeth except i1 and i2 and i3	Deseado
Mandible, with milk-teeth (No P13,366)	Deseado
Mandible, with milk-teeth (No P13,344)	Deseado
Mandible, fragment, with p3 and p4	Deseado
Atlas (No P13,349)	Deseado
Atlas (No P13,291)	Deseado
Atlas (No P13,344)	Deseado
Cervical vertebra (No P13, 477)	Deseado
Cervical vertebra (Field No 662)	Deseado
Cervical 1, dorsals 2, lumbar 3 (No P13, 573)	Deseado

In addition there is a fine specimen from the Colhué-huapi which, in the absence of skull and teeth, is here tentatively included in *Parastrapotherium*. The bones of this individual are all remarkably free from crushing or distortion.

In the American Museum there is a very large skull in good preservation and various fragments, from the Deseado beds.

DENTITION

As the premaxillae have not been found, it is impossible to state with certainty whether upper incisors were present,

but there is no reason to assume that they were The dental formula is. i_3^1 , c_1^1 , p_3^3 , m_3^3 .

Upper Teeth.—*Incisors* were presumably absent. The *canine* is a formidable tusk, differing much in relative size in various individuals, no doubt a matter of sex The tusk grew persistently throughout the lifetime of the animal, the pulp cavity remaining widely open in the oldest individuals The exposed part of the tusk is slightly decurved and is of trihedral cross-section, with broad anterior face and narrowing to a bluntly rounded posterior border The enamel is longitudinally ribbed and fluted and is continuous around the tooth except on the anterior face, where dentine is broadly exposed The distal end of the anterior face is obliquely worn by abrasion of the lower tusk, which keeps the postero-inferior angle sharply pointed, and thus adds much to the effectiveness of the tusk The *premolars*, three in number, are much smaller and of simpler construction than the molars The foremost of the series (p_2) is very small and is frequently lost in the full-grown skull P_3 is likewise very small, its outer wall is convex and is surrounded on all sides, except the masticating edge, by a raised border, internally, there is a single conical cusp, connected with the outer cusp, but, no doubt, separate in the unworn tooth, and eccentric in position, being in advance of the middle of the crown The cingulum runs all around the tooth and is especially prominent on the anterior and posterior faces, where it encloses small pockets

The last premolar (p_4) is much larger than p_3 , but hardly half the size of a molar, its pattern differs from that of p_3 only in minor details, the external wall has a broad and prominent rib, or style, which broadens upward, until, at the base of the crown, it occupies the entire antero-posterior breadth. The style divides the outer surface of the tooth into narrower anterior and much broader posterior portions The style is subject to much individual variation, and is better developed in some specimens than in others, which may, perhaps, be a specific rather than an individual character. The internal conical lobe is connected with the outer wall by an oblique

crest, behind which is a deep valley. The cingulum is visible, though not prominent, but on the outer side it seems to be entirely lacking.

The *molars* changed remarkably during the lifetime of the animal in actual and relative size, in proportions and in the pattern displayed by the masticating surfaces. These striking changes, which also occur in *Astrapotherium*, are due, in the first instance, to the shape of the teeth and, next, to the varying depths of the crests, spurs and crochets; valleys and lakes are, as it were, impressed in the crown, or rise above the base, and are successively obliterated by abrasion. The crowns broaden transversely and increase in antero-posterior length upward, in the upper molars, and downward in the lower and thus the masticating surface grows longer and wider with abrasion. After a certain amount of the crown has been worn away, in the first and second molars, it contracts toward the roots and thus suffers a reduction in antero-posterior length, but not in width, with further wear. The third molar differs from the others in that there is no contraction at the base and that the length of the masticating surface increases actually and still more porportionally until extreme old age. These changes are so striking as easily to mislead one into supposing that several species are indicated by the differently aged individuals of a single one.

The first and second molars are very much alike in construction, while the third differs from them in a similar fashion to the corresponding tooth of a rhinoceros. Indeed, it has frequently been asserted that the molar teeth of the *Deseado* and *Santa Cruz* genera of this family are rhinocerotid in type, but the likeness is superficial and chiefly concerns the trigonal shape of the m_2 . M_1 and m_2 differ somewhat in size and often, seemingly, in construction, but the difference is more apparent than real and is occasioned by the fact that m_1 is erupted very early and is usually considerably worn before m_2 comes into use and is, of course, still farther abraded, when m_3 is erupted. In one particularly fine set of upper molars (No. P13,504) m_1 is much worn, though not

sufficiently to obscure the masticating pattern; m_2 is somewhat abraded, but very much less than m_1 , while m_3 was still in the jaw and shows no sign of wear

The second molar (m_2) displays the structure most unmistakably and may therefore be described first. The large external wall is divided by the prominent anterior style into two very unequal parts, of which the posterior is many times larger than the anterior, which, as in the rhinoceroses, is no more than the raised anterior border of the crown and the groove between that border and the style. The posterior part is smoothly convex and its lower, cutting edge is in two scallops, the hinder one much the larger, which meet in a sharp point on a line with the posterior transverse crest, the external cingulum is faintly marked. On the hinder face of the tooth, the enamel is reflected over from the inner and outer sides, but leaves exposed a triangular area of dentine, placed near the postero-external angle. This triangle is broad at the base, where it covers most of the width of the tooth and narrows to the apex, which is at the opening of the posterior valley. On the external side, the enamel covers all the exposed part of the crown, even extending into the alveolus, but this is obviously because the tooth is not fully protruded from the socket, as is shown by comparing it with m_1 . On the inner side and on the posterior side, beside the triangle already mentioned, there is a broad, basal band of exposed dentine.

The masticating surface is so little worn that the plan of construction is perfectly clear. Two transverse crests run inward from the external wall, of which the anterior one is much the longer, making the anterior half of the crown wider than the hinder part. The anterior cross-crest is so curved that part of it has a fore- and aft-course parallel with the wall. Between the two crests is a valley, which is narrow internally and would be very large along the wall, were it not obstructed by two accessory projections. One of these is a prominent spur extending from the external wall, obliquely inward and backward: the other is a crochet which extends

forward from the posterior crest, almost meeting the spur. The valley is thus divided into three parts, two external pockets and a transverse cleft, which opens inward, or lingually, between the cross-crests. The posterior crest has a very short transverse part and almost immediately curves back parallel with the wall and encloses with that a posterior valley or pocket. The cingulum is prominent on the anterior side of the tooth and on the interior side over the foot of the anterior crest, ending against the posterior one.

The first molar (m_1) displays all the elements described for the second, but the pattern is considerably modified by abrasion. The posterior valley has been converted into an enamel lake and the postero-external part of the main valley has almost been converted into a lake, spur and crochet nearly meeting. In a still older tooth, further worn down by abrasion, the lakes, with spur and crochet, have been removed and the valley is simplified, running toward the buccal side and then obliquely forward. In that condition the tooth remains, until, in extreme old age, all traces of pattern have been destroyed and there remains only a concave area of dentine with surrounding enamel border.

The third molar (m_3) is, in shape, very much like that of a rhinoceros, having the trigonal shape of the latter, with the base of the triangle forward and the apex behind. This shape is produced by the connate outer wall and posterior crest. In this tooth calcification is incomplete and the roots have not been formed, not the least indication of wear is to be seen, for the crown was still concealed in the gum. On the anterior face is a triangular area, where the enamel is lacking, which corresponds to the similar triangle on the approximate face of m_2 . The enamel does not cover the external side of the valley, which is, of course, the outer, or buccal, wall of the crown; the thin edge of the enamel layer may be distinctly seen along the cutting edge of the wall. This is not due to incomplete development, for, in an old and deeply worn molar, it is plain that the outer side of the valley is not enamel-lined, while the inner side, formed by the anterior transverse

crest, is so covered. The cingulum is absent from the outer wall, but is strongly developed on the front, inner side, and on the rear, where it is notched by the opening of the valley, beneath which it bends down as a broad U between the two posterior roots. This tooth has but one transverse crest, which curves backward from its point of origin, the posterior crest being confluent with the external wall. The spur from the wall projects very prominently and nearly meets the transverse crest at its hinder end, narrowing the valley to a slit. The spur diminishes in prominence upward and, in an old tooth, it is nearly removed by abrasion, leaving the valley open almost as long as any trace of pattern remains.

Aside from the lesser number of premolars, the chief difference in the upper teeth between *Astrapotherium* and *Parastrapotherium* is to be seen in the form of the last molar. In the latter genus the spur from the external wall projects inward, nearly reaching the transverse crest, but in the former it is much longer and recurved, running between the crest and the wall and parallel with them. This slight change gives the tooth a very different appearance in the two genera. In m_1 and m_2 there are even slighter differences, which can hardly be expressed in a description and yet are plain to the eye.

Lower Teeth.—In none of the mandibles from the Deseado are any of the permanent *incisors* preserved. The *canine* displays some significant differences from the lower tusk of the Santa Cruz species, though the two are much alike in form. The tusk is curved almost in a semicircle, but does not, like the superior one, retain throughout life the wide-open base, but, in old age, contracts toward a root and closes the pulp-cavity distally, in one individual, only a small, central nerve-canal remains above the pulp-cavity. The anterior border is narrowed by a broad, shallow groove on each side, and, externally, there is often, but not always, a longitudinal convexity, hollow internally, into which the pulp-cavity extends and thus gives the tooth a trefoil-like cross-section, which tends to flatten out toward the base. Whether the

presence or absence of the trefoil is a sexual, or a species character is not yet determinable, but nothing of the sort has been observed in the Santa Cruz fossils

Of one unworn lower canine, the enamel is lacking on the anterior and posterior borders, except near the apex, and the exposed area of dentine broadens toward the base. On the lingual side, near the anterior border, the enamel is prolonged, as a gradually narrowing band far within the socket and the much wider part, near the posterior border, comes to an abrupt end a little within the alveolus. Between the two enamel-bands is a narrow, triangular area of exposed dentine. On the outer side, the enamel ends downward in a broad, rounded margin and has no such extension along the anterior edge, as is seen on the inner side

Mandible No P13,365 is interesting in certain respects, the animal was adult, for all the teeth were in use, yet not old, for the hinder crest of m_3 is very little worn. The lower canine is different from any other individual that I have seen, whether isolated or in place, it is relatively very small, compressed and thin, the ratio of antero-posterior to transverse diameter being as 3 to 2. The tusk is erect in position and shows no tendency to turn outward. The tooth is not abraded at all, which seems very strange in view of the animal's adult age, the apex is covered with enamel, except on the hinder side, where a small, triangular area of dentine is exposed. Then, for a short space, the posterior side is enamel-covered and below this begins another enamel-free triangle, which broadens downward to the alveolus. On the anterior border, the enamel ceases below the enamel-sheathed apex and an exposed area of dentine begins, which widens downward as far as the tusk is visible. There can be little doubt that this jaw belonged to a female, but, even so, the entire absence of abrasion is a puzzling circumstance.

The lower canine presents a difficult problem of abrasion; the tooth occludes in front of the upper canine, as ~~is~~ the normal arrangement, and its *posterior* face is extensively worn by contact with that tooth, but the remarkable thing is that

the *anterior* face of the lower tusk is as much and as regularly worn as the posterior. Frequent, but not so universal, is the presence of one or more transverse grooves of wear on the anterior face and it is the abrasion of this face, where no other tooth could have reached it, which is so difficult to account for. In some way, there must have been some systematic and general habit of rubbing the tusks against the ground, or against the trunks of trees and, if so, the supposed proboscis must have been curled up out of the way. Perhaps, the tusks were regularly employed in rooting, but, whatever it was, it was not an exceptional, or individual habit, for I have seen no lower tusk of the Deseado, Colhué-huapi, or Santa Cruz formations, if it was worn at all, that did not have an abraded anterior face. Digging and rooting might account for the longitudinal abrasion, but would not explain the transverse grooves, which, though common enough, are not so general.

In the young animal, the lower canines are erect, but, with advancing age, they become more and more everted, until, in the old animal, with well-worn molars, they are directed much more outward than upward and have a decided resemblance to the tusks of the Wild Boar.

The *premolars* exceed those of the Santa Cruz genus by one, the only examples of this additional tooth which I have seen are in the two rami of a fragmentary mandible (No P 15,067) in which p_3 is almost fully protruded, but not abraded and p_4 is about half-way erupted. The anterior one of the temporary premolars, dp_2 , is not represented in the second dentition, but dp_3 has a successor, which *Astrapotherium* has lost. This permanent tooth, p_3 , bears considerable resemblance to p_2 in *Albertogaudrya*, the Casa Mayor Eocene ancestor of the astrapotheres. The crown is a simple, compressed, sharp-pointed and slightly recurved cone, somewhat eccentric in position, the apex being a little in advance of the middle. Transversely, the tooth is rather thick, the ratio to antero-posterior diameter being as 12 : 17. A faintly marked enamel ridge passes down the anterior side of the cone, which is slightly convex, to a junction with the cingulum

The posterior side of the cone has a concave outline and the enamel ridge is much more prominent than that on the front side and runs down with perfect continuity into the cingulum, which is very high at that point and encloses a basin, or pocket. The cingulum slopes downward from the outer to the inner side of the tooth, where it is conspicuous all around the inner and anterior sides, ending abruptly at the antero-external point. The tooth is implanted by a single stout root, which shows signs of having been formed by the fusion of two. The root passes obliquely downward and forward into the jaw, giving the crown a backward inclination.

The last premolar (p4) is imperfectly molariform, it consists of two crescents, one behind the other, of which the anterior one is the larger, reversing the proportions seen in the molars, in which the posterior crescent is much the larger. The anterior face is covered with enamel, except near the base, where a small triangle of enamel-free dentine appears.

The *molars* increase regularly in antero-posterior length from the first (m1) to the third (m3). I have seen no unworn example of m1, which was erupted so early that it was well abraded before m3 came into use at all, as is also true of the upper molars. So far as may be learned from the worn examples of this tooth, m1 resembles m2 except in being smaller and in having no enamel on the anterior face. M2 and m3 are narrow and compressed and have a decided resemblance to those of the supposedly aquatic rhinoceros, *Metamynodon*, of the North American and Mongolian Oligocene. These molars have the characteristic pillar in the hinder crescent, which was, no doubt, also present in m1 until removed by abrasion. This pillar is larger and more separate from the crescent than it is in *Astrapotherium* and is subject to considerable variation, which seems to be individual rather than specific. In some individuals, the pillar is single, in others it is double, the hinder one much the shorter of the two, and, in others again they are both of nearly equal height, but I have seen none in which it was absent altogether. Considering the apparently trivial nature of this element, its constancy among nearly all groups of indigenous South American ungulates is surprising.

In *Astrapotherium* the lower molars are closely similar to those of the *Deseado* genus, the crown consists of two crescents, one behind the other, the posterior one of which is much larger and lacks the anterior horn, its place being taken by the internal pillar. For most of its height, this pillar is connate with the crescent, but, in unworn teeth, its apex is separate. In *Parastrapotherium*, the pillar is very much more distinct and remains separate till a more advanced stage of wear. In the Litopterna, as in the Astrapotheria, the pillar tended to a reduction and final disappearance in the more advanced members of the order, such as *Thoatherium*.

MILK DENTITION

The temporary teeth are well represented in the collection, except the incisors and canines, for the cheek teeth the formula is $dp \frac{2}{3}$ and I can find no evidence of more than three milk-premolars above, or below.

Upper Teeth —The foremost deciduous premolar (dp_2) is like no other tooth in either series, but most of the evidence of pattern on the masticating surface has been removed by wear. On the external wall are three vertical ridges, or styles, anterior, median, and posterior, bounding two shallow concavities. The anterior style projects forward as a distinct lobe, which is not more than half as wide transversely as the remainder of the tooth and, behind the posterior style the external wall is extended as a nearly flat surface. The external cingulum is conspicuous, more so than on the other teeth, deciduous, or permanent, it curves down continuously into the anterior and median styles, of which the latter is grooved in the upper portion. Internally, the crown has two lobes, in the hinder one of which is a minute enamel-lake. What these lobes were like before abrasion, it is difficult to say. Despite this elaborateness of pattern, the tooth is very small.

The second milk-premolar (dp_3) is very much larger than dp_2 , especially in antero-posterior diameter, and is more nearly molariform, though much smaller than any molar; the external wall resembles that of the molars. The anterior trans-

verse crest follows a V-like course, first passing obliquely inward, where it forms a rounded lobe, then bending outward, to join the wall, thus enclosing a small, anterior enamel-pocket, which is narrowed by a spur, projecting inward from the wall. The posterior transverse crest is short and straight and ends internally in a convex lobe, like that of the anterior crest; the lobe sends off a backward ridge, parallel to the outer wall, with which it encloses the posterior enamel pocket. When abrasion has proceeded somewhat farther, the inner half of the crown appears to consist of two V-like crests.

The last deciduous premolar, dp_4 , shows but little sign of wear, but is, unfortunately, cracked and fissured in such a way as to obscure some of the pattern. This tooth is very much larger than dp_3 and has the principal elements of a molar, though somewhat differently arranged. The anterior border is curved outward and forms a raised ridge between which and the anterior style is a deep vertical groove, which, with the ridges, is much better marked than in dp_3 . The relatively very large postero-external lobe has a low, yet distinct, posterior style, somewhat more than halfway to the hinder border. The anterior transverse crest passes directly inward, without backward curvature, and the posterior crest is very short, ending in an internal peak, from which descends a posterior ridge parallel with the wall. The valley is much more widely open internally than it is in the molars; there is a short spur from the outer wall which joins the posterior crest and encloses with it a deep fossa and this, after abrasion, becomes an enamel lake. The posterior valley is divided by a longitudinal ridge which is tuberculated. This tooth is, thus, rather simpler than the molars.

Lower Teeth.—The formula is $\cdot d_1\bar{3}, dc1, dp\bar{3}$. The only *milk-incisor* preserved is the external one, $d_1\bar{3}$, which has a very different shape from that of its successor, $i\bar{3}$. It is much wider transversely in proportion to its antero-posterior diameter, the crown is bilobate, made so by a notch of the cutting edge, but the median groove on the dorsal, or posterior, face of the procumbent tooth is hardly perceptible. The

basal cingulum is prominent and tuberculated and forms a raised border, which runs around the periphery of the crown in continuation of the cingulum, making the dorsal face concave

The milk-canine is lost or broken away on both sides, but was manifestly small. The three milk-premolars increase regularly in size from the first to the third and are molariform, except that dp_2 is incompletely so, the anterior lobe is hardly a crescent, because the internal valley is so shallow. Dp_3 has a deeper anterior valley, but it is shallower than in dp_1 . In a less abraded tooth (No. P 13,344) the pillar in the valley of the posterior crescent may be seen as a spur from the outer wall, with which it has been connected by wear. Dp_1 differs in no important respect from a molar, the posterior crescent is unworn and the pillar in its valley is still free from the wall

SKULL

The only skull in the collection (No. P 13,329) is a crushed specimen, of which the top has, for the most part, been weathered away, the premaxillae have been lost. Otherwise, the bony palate, the upper teeth and the *basis cranii* are in an excellent state of preservation. This skull is not very much larger than that belonging to the Field Museum skeleton of *Astrapotherium magnum* (No. P 14,251) and does not differ from it in any notable way. Certain apparent differences may very well be due to the different directions of the compression which the two skulls have undergone, one being much crushed and flattened vertically, the other slightly crushed and narrowed laterally. The principal differences, other than size, that I can detect between the two skulls are (1) that in *Parastrapotherium* the palatine plates of the maxillaries are separated by a long, narrow triangular slit which extends as far back as the middle of mI . Lacking the premaxillae, it is impossible to say just what the significance of this opening may be, nor whether it may not be one of the results of vertical compression. In view of the regular, symmetrical shape of the fissure and the absence of any shattering in the bony

palate, it seems very unlikely that the structure can have resulted from crushing. If this long fissure is natural and normal, it would seem to show that the premaxillaries had very elongate and slender spines. (2) There is a difference in the shape of the post-glenoid and paroccipital processes, which, in *Parastrapotherium*, seem to be shorter, heavier and more massive, but this difference may be illusory and due to compression.

Vertebrae of this genus may be most conveniently dealt with in connection with the material from the Colhué-huapi beds, but the manus is well represented by two specimens, presumably of the same individual, in the National Museum in Buenos Aires, casts of which are in the American Museum (No 11,729)

MANUS

(Pl. V, Fig 2)

The Buenos Aires feet, just alluded to, are labelled *Pyrotherium romeri* and that of the right side appears to be the one figured by Ameghino (*Bol Inst. Geogr. Argent*, T. XVII, 1897, p 442, Fig 15) This is, perhaps, another individual, or else the drawing is very inexact; on the other hand, it would be a surprising coincidence to find three specimens of the manus, all of them lacking the lunar. In September 1901, I photographed in Dr Ameghino's house in La Plata the same fore foot which he had previously figured as belonging to *Pyrotherium*. Tournouer referred this foot to *Astrapotherium* (not admitting *Parastrapotherium* as distinct). Both casts in the American Museum have lost the lunar and this makes the proper assembling of the carpals exceedingly difficult, as all the bones are immovably fixed. Phalanges are entirely wanting and only the proximal end of the first metacarpal is preserved.

Without the phalanges, the manus is broad and short; these proportions are exaggerated in the *Carpus*, the elements of which are heavy and block-like, resembling those of an elephant in general aspect, though not in the details of shape

and proportions. The *scaphoid* is one of the larger bones and its proximal surface, that for the radius, is convex palmo-dorsally, narrowing much toward the radial side. Distally, the scaphoid rests upon the trapezium and trapezoid, but does not extend over upon the magnum, with which the distal part of the bone has a considerable lateral contact.

Judging from the articular surfaces on adjoining carpals, the *lunar* must have been very large and have had an unusual shape, which it is difficult to reconstruct, the downward and forward extension over the magnum being very peculiar.

The *pyramidal* is a large bone, especially in transverse width, though the proximo-distal dimension is small. The proximal facet for the ulna is concave palmo-dorsally, but becomes less so toward the ulnar side, the dorsal face shortening in that direction, nearly the whole palmar side is taken up by the facet for the very large pisiform. Distally, the pyramidal rests for less than half its width upon the unciform, for it has an extensive contact with the fifth metacarpal and extends toward the ulnar side even beyond the latter.

The *pisiform* looks like the calcaneum of a large mammal, the proximal portion is very wide and has facets for the ulna and pyramidal, which are nearly plane and meet at a right angle. The projecting portion is hardly half as wide as the proximal expansion, it is very short and heavy, with rugose distal border.

The *trapezium* is relatively elongate proximo-distally, narrow transversely, the dorsal face is sub-triangular, with apex at the proximal end, where it has a small, obliquely lateral facet for the scaphoid, the distal end is broad and has a corresponding surface for the first metacarpal and, on the ulnar side, is an elongate surface for the trapezoid.

As in the trapezium, the principal diameter of the *trapezoid* is proximo-distal and it is narrow transversely. The dorsal side is rectangular and the proximal end, which articulates with the scaphoid, is somewhat convex. On the sides there are facets for the trapezium and magnum respectively, but it would not seem to have been in contact with the lunar, it

is impossible, however, to make sure of this from the cast, with its immovable carpals. Distally, the trapezoid articulates only with the second metacarpal, of which it covers only about half of the width.

On the radial side, the low, broad *magnum* is hardly half as long proximo-distally as it is on the ulnar side and, on both sides, it is very much shorter than the trapezium or trapezoid. The proximal end, which articulates with the lunar, slopes down steeply toward the radial side, on which is the facet for the trapezoid; that on the ulnar side, for the unciform, is much larger. The distal end, which rests upon the heads of the second and third metacarpals, makes a continuous curve.

The *unciform*, which is the largest of the carpal elements, save, perhaps, the lunar, is very broad and short; proximally, it is covered by the lunar and, more extensively, by the pyramidal; externally, it articulates with the magnum and, distally, it rests upon a projection from the third metacarpal and upon the whole width of the fourth. The contact with the fifth metacarpal is lateral rather than distal, the metacarpal curving around the ulnar side to a contact with the pyramidal.

The *Metacarpus* consists of five members, which, though very short, are rhinocerotid rather than elephantine in proportions. Of the *first metacarpal* (mc. I), only the proximal end is preserved, it is stout and rugose and would seem to have been functional, apparently, it articulates only with the trapezium and is widely removed from the trapezoid and second metacarpal, though by no means so widely as in Tournouer's figure.

The *second metacarpal* (mc. II) is very much broader and, presumably, longer than the first, it is broad and antero-posteriorly compressed, but would seem not to have been so thin and plate-like as in *Astrapotherium magnum*, but as the bones are fixed in the supporting mount, it is impossible to determine their thickness. Most of the proximal end is covered by the trapezoid, but a narrow surface is taken up by the surface for the magnum. The shaft is broad and rugose

and the distal trochlea is very low and much narrower than the distal end of the shaft, which is broadened by the processes for the lateral ligaments

The *third metacarpal* (mc III) is a little longer than mc II and decidedly narrower, most of the proximal end is covered by the magnum, but a process on the ulnar side projects slightly over the head of mc IV to an oblique contact with the unciform. The distal trochlea is broader proximo-distally than that of mc II and the processes for the lateral ligaments are very low and inconspicuous

The *fourth metacarpal* (mc IV) is much shorter and heavier than mc III, the proximal end articulates with the unciform and is somewhat broader than the upper part of the shaft, which, however, broadens much distally, with prominent processes for ligamentous attachment, and the trochlea is much broader than that of mc III

The *fifth metacarpal* (mc V) is very peculiar and, in shape, unlike any of the others. The head has a very narrow lateral contact with mc IV and the surface for the unciform is a broad concavity, much more lateral than proximal in position, truly proximal is a broad surface upon which the pyramidal rests and which is on a level with the proximal side of the unciform. The shaft is exceedingly broad, more than twice as wide as that of any of the other metacarpals and more than twice as wide as its own distal trochlea. The ulnar border of the shaft is irregularly curved and has a prominent rugose projection not far below the proximal end. The radial border is nearly straight, except for a rugose projection corresponding to the one on the ulnar side, and a very conspicuous process for the lateral ligament, near the distal end. The distal trochlea differs from that of any of the other metacarpals in being less convex and in having its proximal border descending steeply toward the ulnar side. This fifth metacarpal has a certain resemblance to that of the ground-sloths, and may possibly mean that the ulnar border of the manus rested on the ground, with the palm turned inward, but, in the absence of phalanges, it is impossible to say what the significance of this resemblance may be.

MEASUREMENTS

	mm
<i>Upper Teeth</i> (No P 13,566)	
Milk-premolar series, length	76
Dp2, ant-post diameter	25
Dp2, transverse diameter	20
Dp2, ant.-post diameter	30
Dp2, transverse diameter	26
Dp4, ant-post diameter	41
Dp4, transverse diameter	36
	mm
<i>Lower Teeth</i> (No P 13,361)	
Di3, ant.-post. diameter	20
Di3, transverse diameter	28
Milk-premolar series, length	72
Dp2, ant-post. diameter	20
Dp2, transverse diameter	12
Dp3, ant-post diameter	24
Dp3, transverse diameter	15
Dp4, ant-post. diameter	34
Dp4, transverse diameter	13

N B The total length of the series is less than the combined lengths of the separate teeth because of overlapping

	No P 13,504 mm	No P 13,329 mm
Upper Cheek-Teeth series, length		228
Upper Premolar series, length		58
Upper Molar series, length		170
P2, ant-post diameter		27
P2, transverse diameter		26
P4, ant-post. diameter	25	32
P4, transverse diameter	35	49
M1, ant-post. diameter	52	52
M1, transverse diameter	47	59
M2, ant.-post. diameter	62	69
M2, transverse diameter	46	64
M3, ant-post diameter	56	67
M3, transverse diameter	49	60

	No P 13,340	No. P 13,291	No 14,351	No P 13,574
	mm.	mm	mm	mm
Atlas, length, ant. to post. cotyles	167	157	127	
Atlas, width over ant cotyles	176	184	149	211
Atlas, width over transverse proc	303	328	232*	
Atlas, width over post cotyles	175	197	147	219
Atlas, ant-post. width of neur arch	80			
Atlas, height of neur canal	62	80		
Atlas, ant-post width, infer arch	54	69	43	
Atlas, ant-post width, transv proc	134		138	

* Approximate

MEASUREMENTS (Cont.)

	No P 11,365	No P 11,492	No P 11,360	No P 13,473	No P 13,147
	mm	mm	mm	mm	mm
Lower Cheek Teeth series, length (approx)	164				
Lower Premolar series, length (approx)	35				
Lower Molar series, length	132	177			
P1, ant-post diameter	25	29			
P1, transverse diameter	20	22			
M1, ant-post diameter	35	49	36		
M1, transverse diameter	23	27	22		
M2, ant-post diameter	45	62	51	51	
M2, transverse diameter	26	24	23	25	
M3, ant-post. diameter	53	62	56	69	
M3, transverse diameter	24	27	28	30	
Lower canine, ant-post diameter	35				
Lower canine, transverse diameter	21		No P 13,329		
Upper canine, ant-post. diameter			47		
Upper canine, transverse diameter			32		

? PARASTRAPOTHERIUM sp.

The individual here considered was collected in the Colhué-huapi formation (*Colpodon* Beds of Ameghina) by the Field Museum parties and, for stratigraphical reasons, was referred to *Astrapothericulus* Amegh., but all the described species of that genus are small and this animal is much more probably assignable to *Astrapotherium*, or *Parastrapotherium*, both of which are reported from the Colhué-huapi and the differences from the *A. magnum* skeleton, described in the foregoing pages, make it likely that the reference should be to *Parastrapotherium*. It is possible that these differences are specific rather than generic, but, as no teeth or skull have been found, a definite decision must await future discoveries.

The individual in question consists of the atlas and axis and two other cervical vertebrae (6-7), 9 dorsal and 4 lumbar vertebrae and the sacrum, pelvis, 2 ulnae and a tibia. The bones are, for the most part, in excellent preservation, usually much better than in the *A. magnum* skeleton from the Santa Cruz (No. P 14,251) and thus serve to clear up certain doubtful matters in connection with the latter. Especially advan-

tageous is the freedom of these bones from crushing or distortion

VERTEBRAE

The *Atlas* of this animal bears considerable resemblance to that of the Santa Cruz toxodont, *Nesodon*, a resemblance that can have nothing to do with relationship. This atlas is much longer antero-posteriorly than in *Nesodon*, but has a similarly great width, which is principally due to the large development of the transverse processes, it also has a notable dorso-ventral height. The anterior cotyles for the occipital condyles are very large and their principal diameter is the vertical one. The neural arch has great antero-posterior breadth and curves upward strongly, to enclose a large neural canal, which is in striking contrast to the small size of the canal in the axis. Near the anterior border of the neural arch, is a large and deep fossa, into the inner end of which opens the foramen for the first spinal nerve and, externally, the fossa opens into the atlanteo-diapophysial foramen. There is no neural spine, not even a rugosity to indicate one. The inferior arch is completely lacking, being broken away and lost, but there remains the broad bar, which extends from the inferior arch out over the transverse process, making the latter very thick posteriorly. This bar forms the posterior boundary of a large, deep fossa, in which is the anterior opening of the vertebrarterial canal. This canal is very large and runs obliquely forward from the posterior border of the transverse process, which it perforates at the base. In front, the atlanteo-diapophysial foramen passes into the fossa and thus connects the deep dorsal and ventral depressions.

The posterior cotyles for the axis are nearly flat and are but moderately oblique to the median line of the neural canal. The transverse processes are greatly developed and give the atlas its width, the outer border of the process is thickened and rugose and describes nearly a quadrant in a regular curve, so that one cannot distinguish clearly between anterior and lateral edges. Posteriorly, the process is abruptly ended and does not extend far behind the line of the posterior cotyles, as it does in *Astrapotherium*.

There is a marked difference in the form of the atlas in this Colhué-huapi specimen and the Santa Cruz genus, in which the transverse processes are not very widely expanded and are produced posteriorly into bluntly rounded tips, which are well behind the plane of the posterior cotyles, and the free border presents laterally much more than forward. Halfway between the great dorsal fossa, into which opens the foramen for the first spinal nerve, and the posterior cotyle, is a small foramen, near the base of the neural arch, which perforates the transverse process obliquely downward and forward, opening into the great ventral fossa. This short canal can hardly be anything but vascular. As was stated above, the transverse processes of the atlas in *Paratrapotherium* are differently shaped, and the vascular canal, just mentioned, is absent.

The *axis* is a large and massive bone and indicates a neck which was very thick both transversely and dorso-ventrally, the centrum is long, broad and depressed, looking much like that of a rhinoceros, but larger than in any existing member of that family. This centrum is keeled, both on the ventral side and along the floor of the neural canal. The keel extends for its whole length along the dorsal side of the odontoid process, where it doubles in width and forms a smooth floor for the transverse ligament; the hinder face of the centrum is deeply concave. The cotyles for the atlas are large and project out prominently from the sides of the centrum, their articular surfaces are continuous with that upon the ventral side of the odontoid. The latter is long, heavy and blunt, contracting but little toward the free end and channelled along the sides, where the dorsal keel, already mentioned, overhangs on each side.

The neural spine is much prolonged from before backward, and its outer surface is roughened by many fine, oblique ridges. The neural canal is surprisingly small, in view of its much larger size in the atlas. The neural spine is very large and quite different from that of *Astrapotherium magnum*, not having such a quadrate outline, when viewed from the side,

its dorsal border is regularly curved, rugose and very thick and broadening posteriorly, where it is grooved, the posterior end of the spine is vertical and forms almost a right angle with the dorsal edge; this end is exceedingly thick. The postzygapophyses are of unusual character, partly because of their great size and prominence, and partly because of their decidedly concave faces and steeply inclined position, for they make an angle of some 45° with the fore-and-aft line of the centrum. The transverse processes have been broken away and lost, but the very large size of the vertebrarterial canal is sufficiently indicated.

The third, fourth and fifth cervical vertebrae have been lost, but the sixth and seventh were obtained in a very good state of preservation

The *sixth cervical* is short, but very broad and heavy in the other dimensions, the anterior face of the centrum is moderately convex, the posterior face deeply concave. The neural arch is narrow antero-posteriorly, but broad transversely and encloses a spinal canal which is decidedly larger than that of the axis. The neural spine has been broken and lost, but the broken base is narrow and the spine itself was evidently weak and probably short. The zygapophyses are very large and conspicuous and, to make room on the narrow pedicles of the neural arch, the anterior pair extend back over the posterior pair, at a higher level, of course, the former are convex, the latter concave, both in an unusual degree. The diapophysial part of the transverse process is rather short, but heavy and conspicuous and the inferior lamella, or pleurapophysis, is a thick plate, extending before and behind and, especially, below the diapophysis. The bridge over the canal for the vertebral artery has been lost, but the foramen was evidently large.

The *seventh cervical* differs from the sixth in several respects, as is normally the case. The zygapophyses and the centrum are much the same, though the latter is shorter and, on the hinder border are two hemispherical pits for the heads of the first pair of ribs. There is a neural spine of

some three inches in length, which is narrow, but fairly stout, and ends in a club-shaped tip. It may be inferred that the sixth vertebra had a similar but somewhat shorter and weaker spine. The transverse processes are much longer than those of the sixth cervical, they are slender and rod-like, of trihedral shape and tapering toward the ends. There is no vertebrarterial canal, but well-developed inferior lamellae depend from the outer ventral borders of the centrum, the presence of these on the seventh cervical is an unusual feature.

The number of *dorsal vertebrae* is not definitely known, but there is no reason to suppose that it differed from the formula found in the Field Museum skeleton of *Astrapotherium magnum*, which is 19, for there is a close resemblance between these dorsals and the corresponding ones of the Colhué-huapi individual, here described. There are the same astonishing shortness and weakness of the neural spines and the same backward inclination of the spines of all the trunk-vertebrae. Further, there is a similar remarkable disproportion between the size of the vertebrae of the neck and those of the trunk, the cervicals being large out of all proportion to the dorsals and lumbar.

The *first dorsal vertebra* is, as usual, very like a cervical in aspect, though differing in important respects. The centrum is still relatively large and opisthocelous and the zygapophyses, even the posterior pair, are of the cervical type, but the articular pits for the heads of the first and second pairs of ribs, which are in their normal position, identify this vertebra as a dorsal. The neural arch is short antero-posteriorly and wide transversely, covering the broad, triangular neural canal, which is very much larger than in the anterior or middle regions of the neck. The neural spine is thicker and heavier than that of the seventh cervical, but not longer and is more inclined backward. That the first dorsal should have a spine no longer than that of the last cervical is a feature which is very unusual in an ungulate skeleton. The transverse processes, given off from the sides of the neural arch, are prominent and very massive, especially

in the dorso-ventral diameter, at the distal end, they expand, to make room for the large concavities, into which fit the tubercles of the first pair of ribs. The size and prominence of these processes are very striking, but they cannot be compared with those of the *Astrapotherium* skeleton, for in the mounting of that, it was necessary to leave the centra of the vertebrae concealed in the matrix

In the anterior dorsal region, the successive vertebrae, so far as they are preserved, become smaller and smaller posteriorly, the transverse processes grow shorter and less massive and the facets for the rib-tubercles become smaller. The neural spines remain extraordinarily short and light. With the exception of *Pyrotherium*, which has proportionally even shorter spines, I know of no other large ungulate in which the spines are at all comparable to those of the *Astrapotheria*. When this peculiarity arose within the order, it is impossible, as yet, to say, for the vertebrae are not known in any of the *Astrapotheria* which occur in formations older than the *Deseado*

In the posterior part of the dorsal region, the vertebrae take on zygapophyses of the lumbar type; in the nearly complete skeleton of *Astrapotherium*, the change takes place with the post-zygapophyses of the 16th dorsal. Assuming that the same is true in the *Parastrapotherium*, of the Colhuéhuapi, then, in that skeleton, the 17th dorsal has both pre- and post-zygapophyses of this type and prominent, rugose metapophyses arise from the anterior pair. In this hindermost dorsal region, the zygapophyses are of the artiodactyl pattern, semicylindrical in shape, so as to form exceptionally strong, interlocking joints and, in the lumbar region, as will be seen, these processes attain a degree of complexity such as is equalled in very few artiodactyls. The neural spines of the posterior dorsals are of more normal character than they are in the anterior part of the thorax, or in the hinder dorsals of the *Astrapotherium* skeleton. Though still very short, these posterior dorsal spines are broader and thicker and altogether more like those seen in the tapirs and rhinoceroses

In the Santa Cruz skeleton, these spines, from the 14th to the 18th dorsals, inclusive, have the posterior border conspicuously emarginated, in a manner which further weakened spines that, one would have imagined, were already sufficiently weak. In *?Parastrapotherium* *sp* there is no indication of these emarginations in such of the posterior dorsal vertebrae as are preserved in connection with the partial skeleton from the Colhué-huapi.

The *lumbar vertebrae*, three of which are associated with the partial skeleton just mentioned, are short, with heavy and slightly opisthocelous centra, of broadly oval cross-section, the neural arch is long antero-posteriorly and the neural canal is low and very wide. The spine is short, very broad from before backward, with thickened and rugose tip, which widens posteriorly and becomes very thick on the hinder edge, where the top of the spine is deeply bifid. None of the lumbar in the *Astrapotherium* skeleton has so broad and stout a spine as this. Near the sacrum, the lumbar spines become much narrower and weaker and the cleft of the posterior border disappears, but the backward inclination persists to the end of the lumbar region. (Pl VII, Fig 2.)

Except in the xenarthrous Edentata, I know of no other mammals which have such elaborate intervertebral articulations as those in the lumbar region of the Oligocene and Miocene genera of the Astrapotheria, though in the entelodonts, or "giant pigs," an extinct artiodactyl family, nearly the same condition recurs. Not only are the zygapophyses semi-cylindrical, as in artiodactyls generally, they are scroll-like, as in the entelodonts, but more complexly so. For example, a post-zygapophysis of an anterior lumbar vertebra is in four distinct portions, though the articular surface is continuous over all of them. Beginning at the dorsal side, there is (1) a convex, longitudinal, semicylindrical segment, below this is (2) a longitudinal concavity, or shallow groove, (3) the external, or lateral, part of the process is a convex segment of a cylinder. (4) The articular surface of this third division is reflected far over upon the ventral side of the

neural arch, thus making the fourth and largest segment of the zygapophysis

It is assumed here that the Santa Cruz skeleton of *Astrapotherium* had lumbar zygapophyses of a type similar to those of the Colhué-huapi specimen, but it is not altogether certain, for those processes are so concealed in the connected vertebrae that it is impracticable to determine their shape.

The metapophyses are conspicuous in the anterior part of the lumbar region, but they diminish in size and prominence posteriorly. The transverse processes, which arise high on the sides of the neural arch and are not given off from the centrum, are surprisingly weak, they are narrow, depressed and plate-like, with distal ends somewhat expanded and having a rounded, thickened border. In the anterior part of the region these processes are straight and have a very slight backward inclination, while in the posterior part they are slightly curved and antroverted.

The *Sacrum* consists of five vertebrae, all of which are in contact with the ilia; the compound bone is large and massive, but the neural spines and the various processes are so broken away, that little that is characteristic remains. The neural spine of the first sacral vertebra seems to have remained separate, while the spines of all the other vertebrae have coalesced into a continuous ridge. The centrum of the fifth vertebra has been broken and lost, but the neural canal is so small as to indicate that the tail must have been short.

One exceptional and enigmatic feature remains to be mentioned, the coalesced transverse processes on each side are extended back as a narrow plate of bone, to the postero-dorsal angle of the ischium, with which it is co-ossified. Seen from the side, the pelvis seems to have two obturator foramina, one above the other. It is impossible to say with certainty, whether this extraordinary feature was also displayed by *Astrapotherium magnum*, for in that skeleton both pubes and ischia have been lost, but the appearance of the sacrum does not suggest that there were any such posterior extensions.

There are several extraordinary features displayed by this

spinal column, the significance of which it is very difficult to estimate, for they are not found in any known ungulates other than the astrapotheres (1) There is, in the first place, the remarkable disproportion in size between the vertebrae of the neck and those of the trunk. Considering size only, it is no great exaggeration to say that *Parastrapotherium* had the neck of an elephant and the loins of an Indian Rhinoceros.

(2) The neural spines of all the vertebrae are astonishingly weak and short, in view of the powerful neck and deep, massive head, one would expect to find, from the analogy of those large ungulates of which the anterior dorsal vertebrae are known, very long spines for the attachment of the *ligamentum nuchae* and the long muscles of the back, but, in this skeleton, they are actually no longer than in a lion, though they are, undoubtedly, thicker transversely. The toxodont genus, *Nesodon*, of the Santa Cruz formation, offers the strongest possible contrast to the astrapothere genera of the Santa Cruz and Colhué-huapi with regard to the spines of the anterior dorsal vertebrae, which are so very long, that they must have produced a hump at the shoulders, much as in the American Bison (*B. bison*).

(3) The transverse processes of the lumbar vertebrae are likewise exceedingly weak, not equalling those of the larger cats in length or breadth, though of somewhat greater actual thickness. This weakness points to an underdevelopment of the *longissimus dorsi* and *psoas* muscles.

(4) The sacro-pelvic articulations are of an extremely exceptional character, not only does the sacrum support the ilia for its entire length, but the fused transverse processes, on each side, give off a narrow, plate-like extension, which is continued back to a junction with the ischium, with which it is co-ossified. This has some likeness to the sacro-sciatic connection in the armadillos, but is produced in a different way.

These characteristics show how very exceptional was the spinal column in the later genera of the Astrapotheria;

nothing is, as yet, known of the vertebrae in the genera more ancient than the Deseado stage, *Astraponotus*, *Albertogaudrya*, or *Trigonostylops*. Possibly, these peculiarities are expressions of an amphibious mode of life

LIMB GIRDLES

(Pls VIII, IX)

In the Colhué-huapi skeleton the *pelvis* is preserved with relative completeness, allowing a determination of all the more important characters. It is very large, with length and breadth almost the same. The ilium has a short, wide peduncle, which is depressed and flattened, not trihedral, the anterior expansion is very wide and has its broad surfaces presenting dorsally and ventrally without any eversion. It can, thus, have rendered no support to the visceral mass, which, behind the ribs, must have been carried by the abdominal walls entirely. This is the primitive position in the early ungulates, which are not too large, as in the North American genera, *Barylambda* of the Paleocene and *Coryphodon* of the Wasatch, whereas in the middle Eocene, the much larger *Uintatherium* has the ilia as strongly everted as in an elephant.

The free border of the iliac plate is very thick, massive and rugose and its medial end is somewhat upturned to articulate with the sacrum, with which it appears to be ankylosed, as it certainly is in *Astrapotherium*. As already mentioned in connection with the sacrum, the co-ossified sacral transverse processes are continued back, on each side by a long, narrow plate, which ankyloses with the ischium. Here is another paradox in the structure of these extraordinary creatures. Not only is the pelvis co-ossified with the sacrum, but an additional supporting buttress runs from the ischium to the sacrum, and must have added materially to the strength of the ilio-sacral joint. Why should such an uncommonly strong joint be found in association with such weak loins, limbs and feet as characterize all this group?

The acetabulum is large, deep and nearly circular in out-

line, the antero-posterior diameter but slightly exceeding the transverse. A long, narrow and deep sulcus invades the articular surface, which, presumably served for the attachment of the round ligament, though the slightly damaged head of the femur in the skeleton of *Astrapotherium* shows no pit for this ligament, it may have been present before the injury was inflicted, but, if so, it must have been very shallow. On the other hand, the two genera may have differed with regard to the presence of the pit.

The ischium is long, the peduncle of its dorsal branch is short, laterally compressed and flat on the inner side, convex on the outer, the posterior expansion is very broad dorso-ventrally, ankylosing at the postero-dorsal angle with the sacral plate as already described, a small, conical tuberosity arises at the junction of the two elements. The opening thus encircled by the ilium, ischium and sacrum, is narrower than the obturator foramen, but with much greater fore- and aft-diameter. The descending branch of the ischium is very broad and the symphysis very long, extending for the whole length of both pubis and ischium. The hinder border of the two co-ossified ischia is a regular, convex curve, with no notch on the median line.

The descending branch of the pubis is rather short, but antero-posteriorly broad, with concave borders in front and behind, the horizontal branch is long and slender, making the posterior pelvic opening very large, which is, perhaps, indicative of its female sex.

The side-view best displays the remarkable peculiarities of this pelvis. (1) Most obvious and most exceptional is the double opening, the obturator foramen below and the long space enclosed by the ilium, ischium and continuation of the sacral transverse processes above. (2) The great length of the pre-acetabular portion of the pelvis as compared with the post-acetabular is a conspicuous feature. (3) The symphysis is exceptionally long and involves the full length of both pubes and ischia; the hinder border is entire, without notch.

LIMBS

The only limb-bones associated with these vertebrae are two ulnae and a tibia, which differ but little from those of the Santa Cruz species

The *Ulna* is a little longer and heavier than in *Astrapotherium magnum*, but the difference is not great and, otherwise, there is little distinction between the two genera as regards this bone, except for one conspicuous feature in *Parastrapotherium*, which is almost certainly pathological. In the ulna of the Santa Cruz *Astrapotherium*, there is, on the external side of the proximal end, a deep channel, which is produced by the infolding, as it were, of the external border and runs for the length of the olecranon, as well, the outer boundary of this channel is rather thin, but strong.

In the left ulna associated with the Colhué-huapi vertebrae, on the other hand, the channel is much shorter and narrower and the external border is a thick, rugose mass, which crowds in upon the channel, reducing its width and almost reaching the articular surface of the sigmoid notch. This roughened mass is continuous with a gentle swelling on the hinder side of the ulna, the whole having a decidedly abnormal look and suggesting an exostosis, though there is no indication of a fracture. It may have been occasioned by an infected wound owing to a bite inflicted by one or other of the great predaceous marsupials, or, perhaps, it was received in fighting with one of its own species, for the great, sharp-pointed tusks might easily have laid open a massive leg. If so, however, this would negative the suggestion made above, from the very wide posterior pelvic opening, that this individual was a female. There is no sign of infection in the joint itself

Unfortunately, the ulna of the opposite side throws little light on this problem, though one small feature may be regarded as conclusive. The part of the bone of the left side which was involved in this pathological process, is, in the right ulna, almost entirely broken away and lost. The latter, however, retains an area on the posterior face, which,

in the left ulna, is swollen, and that area has an entirely normal appearance. The articular surfaces for the humerus, the coronoid process and the olecranon are almost exactly the same in the two genera, though everything is broader and heavier in *Parastrapoterium*. There is also a difference in the proximal articulation of the ulna with the radius, in the latter genus the head of the radius articulates with the anterior side of both of the proximal facets for the humerus, each of which has an articular band for the radial head. In the Santa Cruz skeleton, on the contrary, there is only one such band, that on the inner projection for the humerus.

The shaft of the ulna is very similar to that of *Astrapoterium magnum*, but rather stouter, and the interosseous crest is much less prominent, though perfectly distinct. The distal end of the shaft is thicker and more roughened and the carpal surface is more distinctly divided into an anterior shallow concavity and a posterior saddle-shaped area, the surface for the pisiform occupies the whole breadth of the palmar side.

The *Tibia* is of nearly the same length as in the Santa Cruz skeleton, but is heavier, and of very similar shape. The facets for the femoral condyles are unequal and of different form, the inner one is narrower and more concave, but is prolonged considerably farther forward, the outer facet is broader and flatter. The tibia cannot be said to have a spine, the two condylar surfaces are not in contact, except near the posterior border, where they are raised into a low prominence and become confluent. The cnemial crest is broad, rough and massive and then, gradually contracting, is continued down for three-fourths of the length of the bone. The shaft is of the usual trihedral shape, becoming of transversely oval cross-section below and broadening at the distal end. The proximal facet for the fibula is in the usual position, but distally, there is no facet. This tibia is in such a state of preservation that a distal articular surface, had one been present originally, could not have been lost or removed. The two bones cannot have been in contact below.

The surface for the astragalus is almost flat and has no intercondylar ridge, or dorsal tongue, but is very faintly and obscurely divided into outer and inner concavities. The internal malleolus is very thick and heavy; the articular surface on its external (or fibular) side, which articulates with the side of the astragalus, is separated from the distal surface, which fits into the astragalar trochlea, but is reflected over upon the distal end of the malleolus, which articulates with the pit on the side of the distal end of the astragalus. Altogether, this is a very peculiar joint

Although there are not many points of direct comparison between the two skeletons, it is evident that they differ only in matters of minor importance.

MEASUREMENTS

	F	M	No	P	13.437
					mm
Atlas, width (approx)					318
Atlas, ant-post length					120
Atlas, transv proc, width from post cotyle					82
Axis, length, incl odontoid					171
Axis, length from ant cotyle					97
Axis, ant-post length of spine (approx)					135
Axis, width over ant. cotyles					128
Axis, width of post face					87
Axis, width over post-zygap					123
Sixth Cervical, length of centrum (approx)					80
Sixth Cervical, length over zygap					110
Sixth Cervical, width of anterior face					88
Sixth Cervical, width of posterior face					110
Sixth Cervical, width over post-zygap					159
Seventh Cervical, length of centrum					61
Seventh Cervical, length over zygap					105
Seventh Cervical, width of ant. face					87
Seventh Cervical, width of posterior face					139
Seventh Cervical, width over post-zygap					170
Seventh Cervical, height of spine from centrum					102
Seventh Cervical, height of spine from top of neur canal					70
Seventh Cervical, neur spine, ant post diameter at tip					20
Seventh Cervical, neur spine, transverse diameter at tip					25
First Dorsal, length of centrum					60
First Dorsal, length over zygap					88
First Dorsal, width of anterior face					85
First Dorsal, width of posterior face					99
First Dorsal, width over prezygap.					182
First Dorsal, width over post-zygap					161
First Dorsal, width over transv proc					260
First Dorsal, height of spine from centrum					117

MEASUREMENTS (Cont)

	F	M	No	P	13	347
	mm					
First Dorsal, height of spine from top of neural canal						79
First Dorsal, neur spine, ant-post diam at tip						32
First Dorsal, neur spine, transv diam, at tip						30
Fourteenth Dorsal, length of centrum						44
Fourteenth Dorsal, width of anterior face						70
Fourteenth Dorsal, height of spine from top of neur canal						68
Fourteenth Dorsal, neural spine, ant-post diam at tip						42
Fourteenth Dorsal, neural spine, transv diam at tip						18
Eighteenth Dorsal, length of centrum						44
Eighteenth Dorsal, width of anterior face						51
Eighteenth Dorsal, neur spine, height from top of neur canal						67
Eighteenth Dorsal, neur spine, ant-post diam at tip						47
Eighteenth Dorsal, neur spine, transv diam at tip						13
Second Lumbar, length of centrum						48
Second Lumbar, width of anterior face						53
Second Lumbar, width over metapophyses						91
Second Lumbar, neural spine, height from top of neural canal						73
Second Lumbar, neural spine, ant-post diam at tip						53
Second Lumbar, neural spine, transverse diam at tip						23
Third Lumbar, length of centrum						52
Third Lumbar, width of anterior face						64
Third Lumbar, width over metap (approx)						90
Third Lumbar, width over post-zygap						69
Third lumbar, neural spine, height from top of neur canal						61
Third Lumbar, neural spine, ant-post diam at tip						69
Third Lumbar, neural spine, transverse diam at tip						35
Fourth Lumbar, length of centrum						52
Fourth Lumbar, width of anterior face						62
Fourth Lumbar, width over post-zygap						65
Fourth Lumbar, transv proc, width at base						57
Fourth Lumbar, transv proc, width at dist end						23
Fourth Lumbar, neur spine, height from top of neur canal						61
Fourth Lumbar, neur spine, ant-post diam at tip						65
Fourth Lumbar, neur spine, transverse diam at tip						34
Fifth Lumbar, length of centrum						48
Fifth Lumbar, width of anterior face						71
Fifth Lumbar, width over metap						93
Fifth Lumbar, width over transv proc						254
Fifth Lumbar, transv proc, width at base						24
Fifth Lumbar, transv proc, width at tip						23
Fifth Lumbar, neur spine, height from top of neur canal						55
First Sacral, width of anterior face						74
First Sacral, width of neural canal (ant opening)						52
First Sacral, height of neural canal (ant, opening)						23
Fourth Sacral, width of neural canal (post. opening)						27
Fourth Sacral, height of neural canal (post opening)						15
Ulna, length from olecranon						473
Ulna, length from coronoid proc						422
Ulna, length from ext. humeral surface						350
Ulna, width over humeral surfaces						92
Ulna mid-shaft, width						52

MEASUREMENTS (Cont)

	F M No P 13.347
	mm
Ulna mid-shaft, thickness	44
Tibia, length, internal side	403
Tibia, length, external side	378
Tibia, proximal width	103
Tibia, proximal thickness	67
Tibia, mid-shaft, width	52
Tibia, mid-shaft, thickness	54
Tibia, distal width	83
Tibia, distal thickness	48

ASTRAPOTHERICULUS Ameghino

Astrapothericulus Amegh *Anal. Soc. Cien. Argentina*, T LI, p. 73, 1901.

The original definition of this genus is as follows.

“Même formule dentaire que chez *Astrapotherium*. Toutes les molaires supérieures et inférieures avec un très fort bourrelet d’émail à la base. Canines supérieures et inférieures, très petites, avec l’émail limité à la partie tout-à-fait antérieure, à croissance limitée et bout fermé. Symphyse mandibulaire non élargie ne aplatie, sinon étroite, haute et avec les canines implantées presque verticalement. Tous les représentants sont de petite taille, jusqu’à maintenant on ne les connaît que de la formation patagonienne [i e., Colhué-huapi]. Type du genre l’*Astrapotherium* Iheringi.”

Of this comparatively rare genus, I have seen no specimens in either the Chicago or the New York collection. There is in the Princeton collection an incomplete mandible, which was obtained by Mr Hatcher at Arroyo Eke and is of uncertain stratigraphical position. If it was derived from the Santa Cruz beds, it is the only known example of such derivation. This individual was figured in the *Patagonian Reports*, Vol VI, Pl XXXV, Fig 1, and agrees perfectly with Ameghino’s description. The genus differs from *Astrapotherium* and *Parastrapotherium*, not only in the respects which Ameghino enumerates in his diagnosis, the rooted canines, both upper and lower, the erect lower tusks, the deep and narrow mandibular symphysis, and the small size of all the species, but also in the very large and conspicuous pillar in the hinder crescent of the lower molars. Were the skull

known, no doubt there would be many additional peculiarities in the list. Stratigraphically, *Astrapothericulus* is intermediate between *Parastrapotherium* and *Astrapotherium*, but not at all structurally, for it is equally removed from both of these genera and does not serve to connect them. It rather represents a separate tribe, or phylum, though probably derived from a common Eocene ancestry, possibly *Astraponotus*, of the Musters stage. The order is traceable back to the Casa Mayor formation, where it is represented by *Albertogaudrya*, as yet known only from jaws and teeth, but, so far as it is known, fitting perfectly the ancestral position, which its geological antiquity suggests. The order is an isolated one, though there are suggestions of a relationship with the Litopterna, but the oft-asserted connection with the Entelonychia is certainly illusory. The skeletons of *Homalodotherium* and *Astrapotherium* collected by Mr Riggs for the Field Museum make it abundantly clear that, aside from the Pyrotheria, no two groups of the indigenous South American ungulates are farther apart than the Astrapotheria and the Entelonychia.

There is much reason to believe that the pre-Pliocene mammalian faunas of South America, which have been collected almost entirely from the Far South of the continent, represent but outlying colonies away from the main course of development. The Santa Cruz fauna is one of the richest and most diversified assemblages of mammals that is anywhere known, yet that fauna lacks many groups which might be expected to occur in it and which, there is every reason to believe, were flourishing in Santa Cruz time in the forested regions of the North of the continent. For example, it is agreed by all students of the order that the South American Edentata or Xenarthra, form a natural, homogeneous and closely inter-related group, yet two of the suborders, the tree-sloths and the ant-bears, are entirely lacking in the Santa Cruz and all preceding faunas. It is impossible to believe that these groups were not already in existence, or that they originated in some other continent and migrated to South

America at a later time. The only alternative is to assume that these animals were living in the tropical and sub-tropical parts of the continent during the early and middle Tertiary. The same considerations apply to several other groups, but it is unnecessary to repeat the argument, suffice it to say that similar facts are several times recorded in the Tertiary history of both North and South America.

Another principle that finds application in the evolution of the *Astrapotheria* is that a very isolated genus, or a small group of such genera, is always a straggler in time or space. An excellent illustration of this is afforded by the peculiarly North American Prong Horn, which is so far removed from all other antelopes that it is placed in a family by itself, the Antilocapridae. That fact suffices to make it probable that *Antilocapra* has had a long North American history and that it is the last survivor of a large and variegated group of related genera. This inference is fully confirmed by late discoveries, which show that, in the North American Pleistocene, the Prong Buck was one of a diversified group of genera, some with two pairs of horns, some with one, some with simple horn-cores, others with furcate cores, most with straight horns, but others with spirally twisted horns like the strepsicerine antelopes of Africa, for which they were at one time mistaken. The family may be traced back to the Pliocene and upper Miocene and the recent investigations of Mr. Childs Frick have brought to light an astonishing and bewildering variety of genera, with two, three, or four horns, simple and straight, furcate, or branching like deer's antlers, of which only a small fraction had previously been known. The isolation of *Antilocapra* and wide difference from all other antelopes of the New or the Old Worlds, is thus accounted for. It is the last survivor of a great group—a belated straggler in time.

Throughout the recorded history of the *Astrapotheria*, from the early Eocene to the late Miocene, one is struck by the lack of variety or diversity among them; at each stage a single genus, or, more rarely, two genera, represent a group

that survived so long and underwent continual change. The contrast between the Astrapotheria and Entelonychia, on the one hand, and the Toxodonta and Typotheria, on the other, in regard to variety and diversification, is most striking and strongly suggests that the principal range of the *Astrapotheria* and *Entelonychia* was far to the north, amid the forests and savannahs of the warmer regions. These animals are to be regarded as outliers, as stragglers in space

PRINCETON UNIVERSITY

EXPLANATIONS OF THE PLATES

PLATE I

Astrapotherium magnum (Owen) right side, Santa Cruz Miocene of Patagonia, No P14,251, Field Museum, Chicago

PLATE II

Astrapotherium magnum (Owen) Drawing of skeleton shown in Plate I (After Riggs)

PLATE III

Astrapotherium magnum (Owen) Skull, left side and front

PLATE IV

Astrapotherium magnum (Owen) Field Museum, No P14,251

Fig 1 Cervical Vertebrae 1-6, from below

Fig 2 Left Scapula, from the front

PLATE V

Fig 1 *Astrapotherium magnum* (Owen) Right Manus, front view Field Museum, No P14,251

Fig 2 *Parastrapotherium* sp Amegh Right Manus, front Mus Argentino de Cienc Nat, Buenos Aires (From a Cast in American Mus Nat Hist, N Y)

PLATE VI

Astrapotherium magnum (Owen) Field Museum, No P14,251

Fig 1 Left Humerus, front view

Fig 2 Left Femur, front

PLATE VII

Fig 1 *Astrapotherium magnum* (Owen) Left Pes, front view (After Riggs)

Fig 2 *Parastrapotherium* sp Amegh Field Mus, No P13,437 Lumbar Vertebra, anterior end

PLATE VIII

Parastrapotherium sp Amegh Field Mus, No P13,437 Pelvis, from behind

PLATE IX

Parastrapotherium sp. Amegh Field Mus, No P13,437 Pelvis, right side

PLATE I



PLATE II

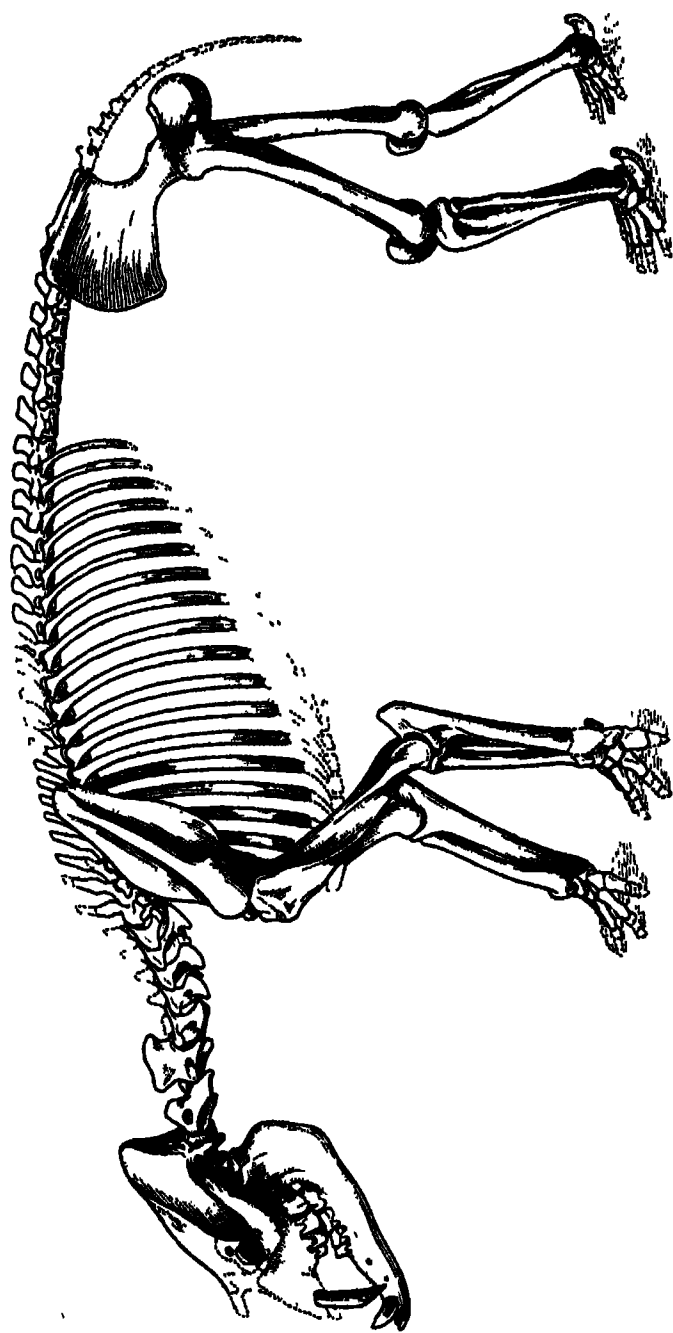


PLATE III



PLATE IV

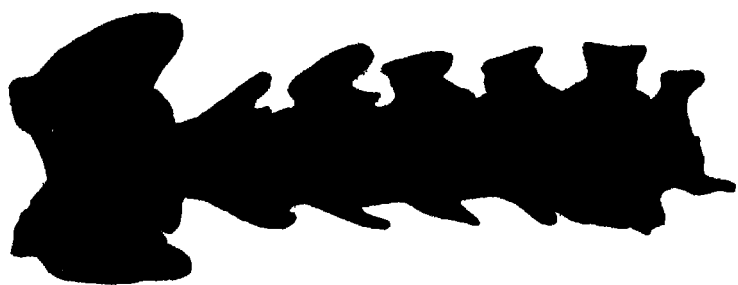


FIG 1

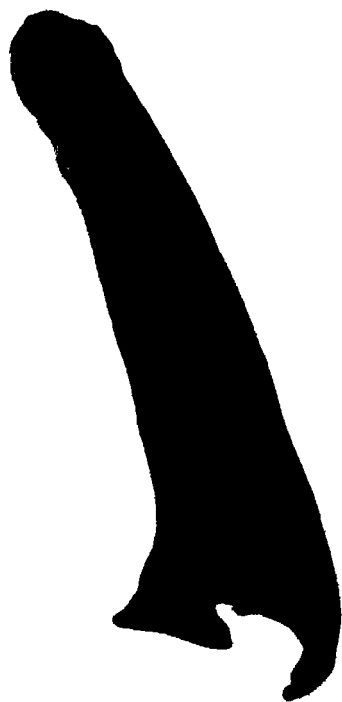


FIG 2

PLATE V



FIG. 1

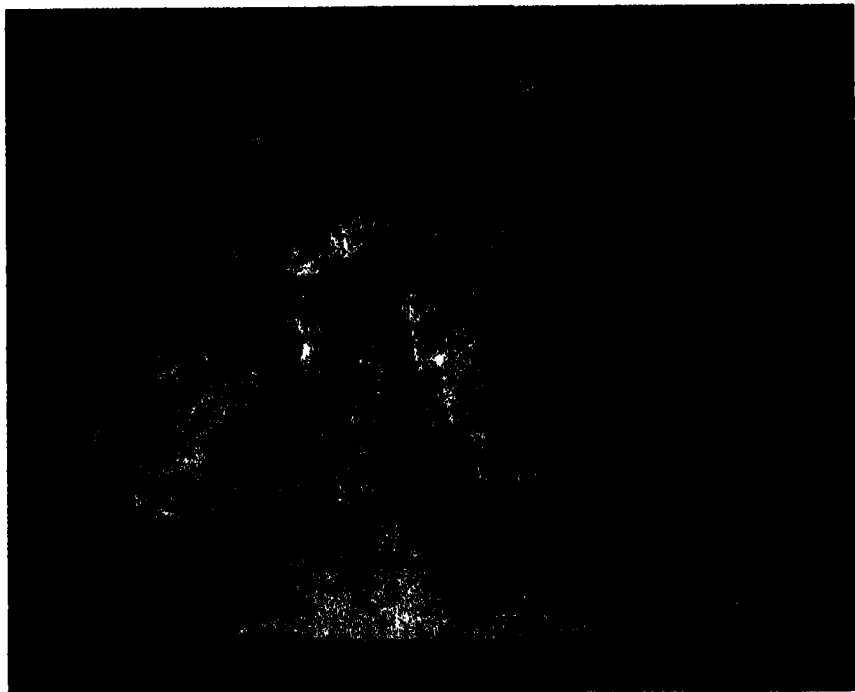


FIG. 2

PLATE VI

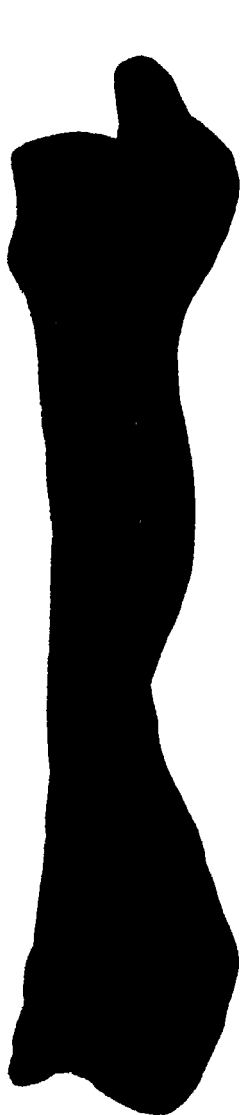


FIG. 1



FIG. 2

PLATE VII

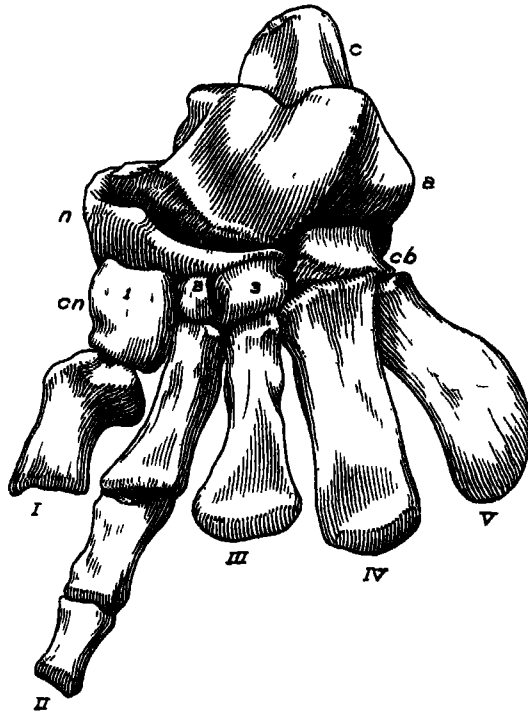


FIG. 1



FIG. 2

PLATE VIII

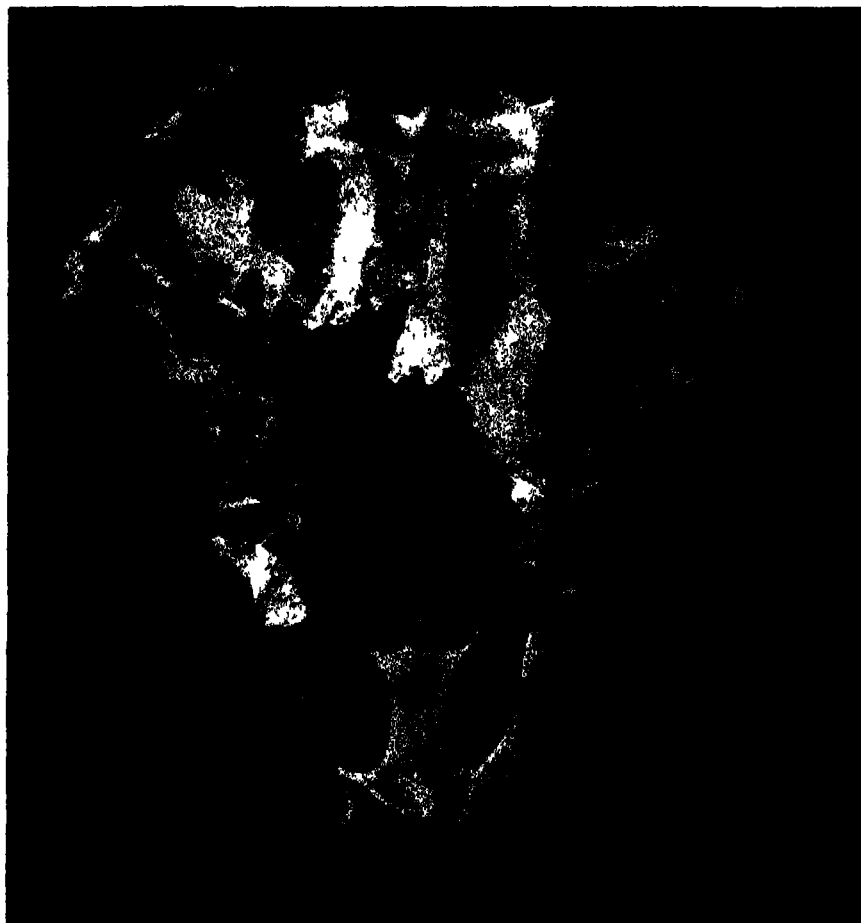


PLATE IX



THE RELATIVE ABUNDANCE OF ISOTOPES*

WALKER BLEAKNEY

ABSTRACT

In this paper a discussion is given of the methods of identifying isotopes with the mass-spectrograph and the difficulties of securing reliable abundance measurements are pointed out. A new mass-spectrograph is described which makes use of many permanent magnets as a means of providing a constant magnetic field. The ion-source used in most of the work is of a new type consisting of an atomic jet ionized by slow electrons. New isotopes of bromine, indium and rhodium were sought and evidence was found for Rh^{101} which presumably accounts for the two periods of decay when rhodium becomes radioactive. Lithium, beryllium and sodium were investigated but no new isotopes were found. Indications of a Co^{57} isotope appeared and this observation was checked by the discovery of a new long period activity induced in cobalt by the absorption of slow neutrons. New isotopes of strontium and barium were found and other isotopes of barium recently reported were confirmed. The relative abundance of these isotopes was also measured. Finally the relative abundances of the isotopes of palladium, iridium and platinum were determined and a comparison made with atomic weights. Only iridium showed a sharp disagreement (192.2) with the accepted value (193.1) of the atomic weight.

INTRODUCTION

THERE are many reasons why an accurate knowledge of the abundance of isotopes is desirable. Very early in the history of isotopes, interest was focussed on the proposition that elements were made up of mixtures of atoms of integral masses taking the hydrogen atom as having unit mass. Later the great work of Aston allowed the chemical atomic weight, that quantity so fundamental in chemical science, to be calculated from the mass and abundance measurements. An independent method was therefore offered to help establish a system of atomic weights of the elements, a task to which Professor Baxter and the late Professor Richards at Harvard contributed so much from their researches in chemistry. Even though the isotopic masses of many elements have not been measured, departures from whole numbers can be safely assumed from Aston's packing fraction curve since its general

* A paper delivered at the Tercentenary Conference of Arts and Sciences at Harvard University, September, 1936

trend seems well established and then an analysis of the relative abundance of the isotopes of an element suffices to compute its atomic weight with surprising accuracy.

Many have been the speculations on the uniformity of the distribution of isotopes in the universe. So far with the exception of the naturally radioactive elements and hydrogen little deviation in the relative abundances has been detected. It is entirely possible however that improved methods may detect such variations and throw considerable light on geological history.

In recent times a complete knowledge of the isotopic species to be found in nature has become of the utmost importance for the interpretation of nuclear transformations produced by artificial means. To the best of our knowledge an atomic nucleus can exist, for any ordinary length of time, in but one energy state. If the state is stable we expect to find the atom in nature, if unstable we do not expect to find its natural occurrence unless its half life is very long or the supply is being continuously replenished from some other reaction. Not only is it desirable to know what nuclear structures are stable but the relative abundance of the isotopes involved in nuclear experiments must also be known in order to determine the probability of any transformation. In the determination of atomic weights only the stronger isotopes are important since the weak ones contribute little to the average weight but in nuclear physics weak isotopes play a much more striking role and measurement of their relative abundance is as important as in the case of the strong ones.

Quantitative knowledge of the stability of nuclei is of course one of the principal objects of present day research. There is a possibility of throwing some light on this question through a quantitative study of the relative abundance of isotopes. Guggenheimer and Elsasser¹ have remarked that the distribution of the abundances of different nuclei corresponds to a thermodynamic equilibrium, from which important conclusions may be drawn once the distribution is known. Sterne² has likewise made some theoretical cal-

culations which illustrate the importance of extending the experimental work.

From these considerations it is apparent that a knowledge of the relative abundances of the isotopes is of great interest to the physicist as well as to the scientists working in related fields

METHODS OF MEASUREMENT

Nearly all of our information concerning the relative abundance of isotopes has been obtained through the study of the hyperfine spectra of atoms, the band spectra of molecules, and positive rays. Of these three methods the last has been the most fruitful and it is of this method that I wish to speak in some detail. In the study of positive rays with the mass-spectrograph the intensities of the ion beams have been measured in two ways. One method relies on the activation of a photographic plate by the impinging particles and when developed in the usual way the blackening of the plate is a measure of the total number of particles striking the point in question. The other method consists in measuring the electrical current carried by the stream of positive rays. Either of these schemes has its advantages and disadvantages. The photographic plate records all the ion beams simultaneously and integrates the effect over the time of exposure but is beset with the difficulty that the density of the image produced on the plate is an uncertain function of the intensity of the corresponding ion beam. The electrical method requires a steady source of ions since the measurements are taken one at a time, the different beams being brought to the collector by adjusting an electric or a magnetic field of the mass-spectrograph.

The photographic technique of measuring the relative abundance of isotopes has been developed to a high degree by Aston, however, when it comes to studying very weak effects the electrical method is probably the superior of the two. Great care must be taken in studying faint isotopes because all kinds of spurious effects begin to emerge of the same order of magnitude as the effect sought. A weak line

may be a "ghost" or satellite of a strong one caused by reflections, inhomogeneity of the fields, lack of perfect focussing and many other defects and the possibility of chemical compounds and impurities must be considered. Those working in this field have learned a number of tests none of which is conclusive separately in all cases, but taken together they are reasonably certain of allowing the correct interpretation to be made. I will enumerate the most important of them. (1) The ion must have the correct e/m as nearly as can be measured and predicted with certainty. (2) The apparent relative abundance of a supposed isotope should be constant over widely varying experimental conditions and good reasons should be known for its behavior if otherwise. (3) The observations should be made in as many different "orders" as possible. (4) If the ionization potential can be measured a link is added to the chain of evidence. (5) The shape of the ionization probability curve is sometimes a distinctive feature. (6) Different chemical compounds may be used as source material for the ions. (7) The relative abundance may be studied as a function of the chemical purity of the sample. (8) Compounds usually preserve the natural abundance ratios to a high degree.

After one is convinced of the identity of the isotopes with which he is dealing, accurate measurements of their relative abundance is another problem. I will mention some of the difficulties encountered without considering how they may be overcome because each particular case is usually a problem in itself. (1) The type of source used for the positive rays may impose a selective effect altering the intensity of the different rays and hence their apparent relative abundance. (2) Space or surface charges sometimes profoundly affect the apparent intensities. (3) If the electrical method is used and the peaks are plotted the question comes up whether to use the relative heights or the relative areas as measures of the relative abundances. For moderate accuracy it seems to make little difference but the best measurements seem to be obtained using a wide slit in front of the collector so that the

peaks have a flat top and observations are made of the relative heights of the peaks. (4) If the photographic plate is used its behavior as a function of the energy of the rays, and the time and intensity of exposure must be accurately known as well as the specific effect of the kind of particles striking it.

Having called attention to the need of accurate abundance determinations and indicated some of the methods and difficulties involved in such measurements I would like to devote the remainder of this paper to some particular results which my colleagues have recently obtained and in which I have been personally interested

APPARATUS

The mass-spectrograph employed for this research was the familiar type in which the ions were produced while practically

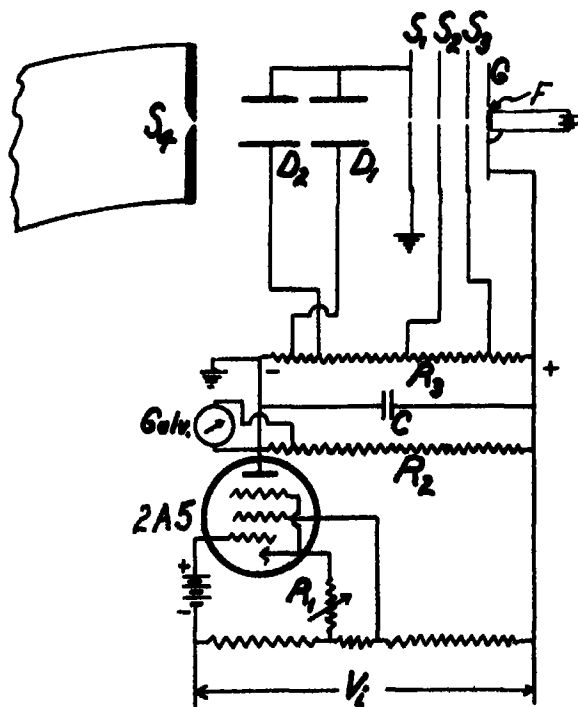


FIG. 1. Diagrammatic representation of the ion source and accelerating system together with the regulating circuit for supplying the potentials

at rest and were then accelerated by a definite amount in an electrostatic field. The arrangement is shown in figure 1, where the circuit for maintaining a very steady potential is also sketched. This nearly homogeneous beam of positive

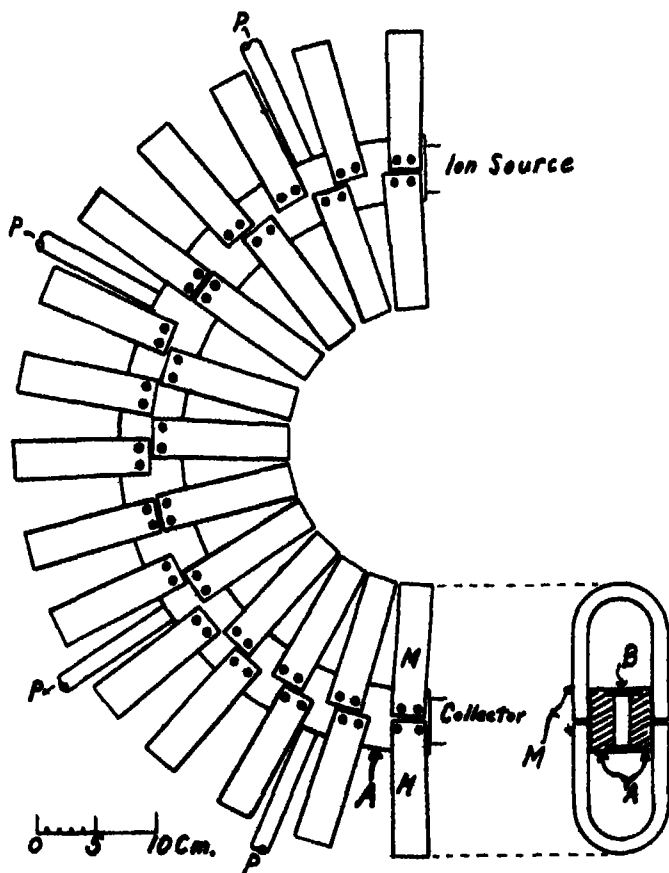


FIG. 2. Arrangement of the magnetic analyzer.

ions entered the magnetic analyzer at S_4 where it was deflected through an angle of 180° . The magnetic system was made up of many small permanent magnets mounted on semicircular soft iron shoes, figure 2. The positive ion current issuing through the exit slit was measured as a function of

the accelerating voltage by means of a sensitive amplifier circuit. Full details of this apparatus have been given by Sampson and Bleakney³

EXPERIMENTAL RESULTS

Bromine, Indium and Rhodium

Positive rays of these elements were obtained by ionizing their vapors with slow electrons. Indium ions were also emitted from a hot filament coated with the oxide of the metal. These three elements are known to absorb slow neutrons and become radioactive. It is believed that in each case⁴ the process is a simple capture of the neutron so that no new element is formed but merely a new isotope of the original element which then exhibits the radioactivity. Activated bromine decays in a manner suggesting the presence of three bodies each having a different half life although only two isotopes have been found. Indium is in the same situation except that in this case two of the activities are sensitive to slow neutrons but the third one is perhaps not. Rhodium, when activated in a similar manner, displays two rates of decay and in this case only one isotope has been identified. It therefore seemed worth while to look for new isotopes of these elements. Blewett⁵ and Sampson⁶ undertook these investigations with apparatus already described. I will quote only the results here. The stable isotopes already known in bromine are Br^{79} and Br^{81} . Hence the expected isotope would be Br^{77} or Br^{83} since the addition of a neutron to Br^{80} or Br^{78} would produce one of the stable nuclei. No new isotopes were found in these positions although 1 part in 3000 of the strong isotopes was thought to be observable. In the case of indium In^{113} and In^{115} are known and one might expect another at mass 111 or 117. None was found in either of these positions when 1 in 10,000 should have been detectable. One is forced to conclude, therefore, that either the process of neutron capture with subsequent activity is not the expected one or that a third isotope in both of these cases exists, it being very weak but having an exceedingly large probability of neutron capture.

Rhodium is an interesting element since its activity is used so frequently as a measure of slow neutron intensity. The half-lives associated with rhodium are 44 seconds and 3.9

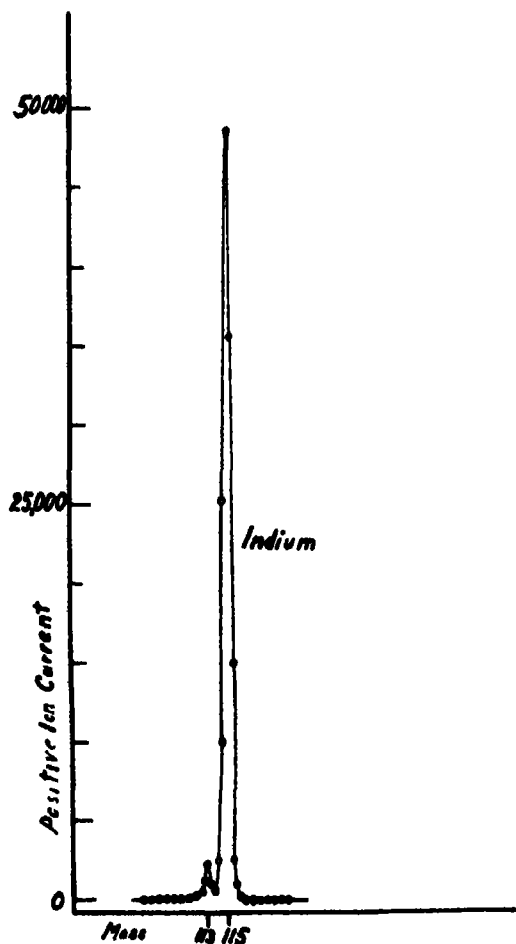


FIG 3 The mass-spectrum of indium

minutes although only the one stable nucleus Rh^{108} has been reported.⁷ The analysis was somewhat complicated by other impurities but reasonably definite evidence was finally found for a new isotope Rh^{101} which falls in one of the expected

positions Its abundance was about 1 part in 1300 of Rh^{103} . Since the activities are both strong and if one activity is to be ascribed to each isotope this means that the cross-section for slow neutron capture is very much larger in one than in the other isotope

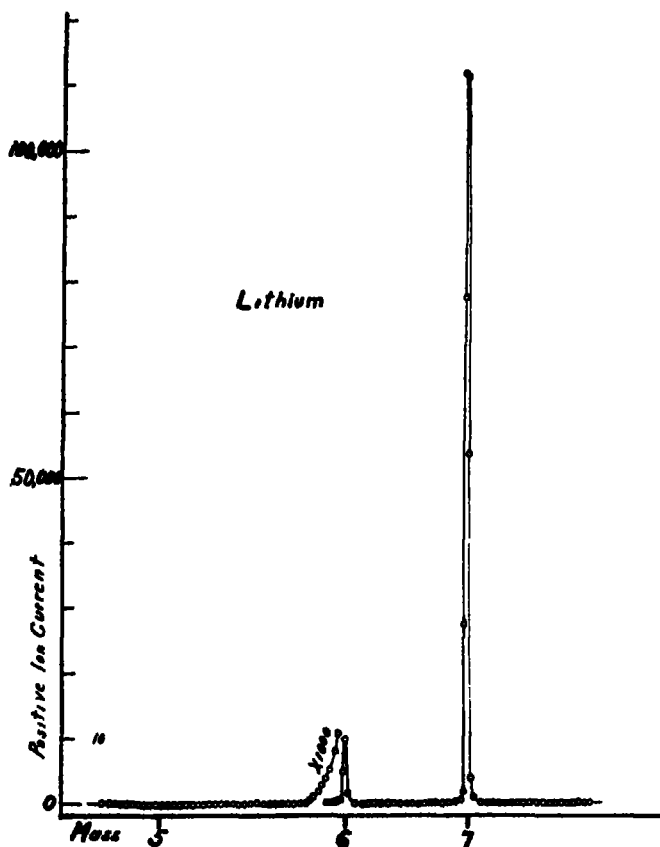


FIG. 4. Lithium ions The mass 5 region is shown magnified 1000 times

Sodium and Lithium

An attempt was made to confirm the existence of Na^{22} and Li^6 which were reported by Brewer⁸ but although our instruments were sufficiently sensitive to detect considerably

smaller amounts than the yield he reported we were unable to find any trace of these isotopes. The results of our analysis are shown in figure 5. We are unable to reconcile

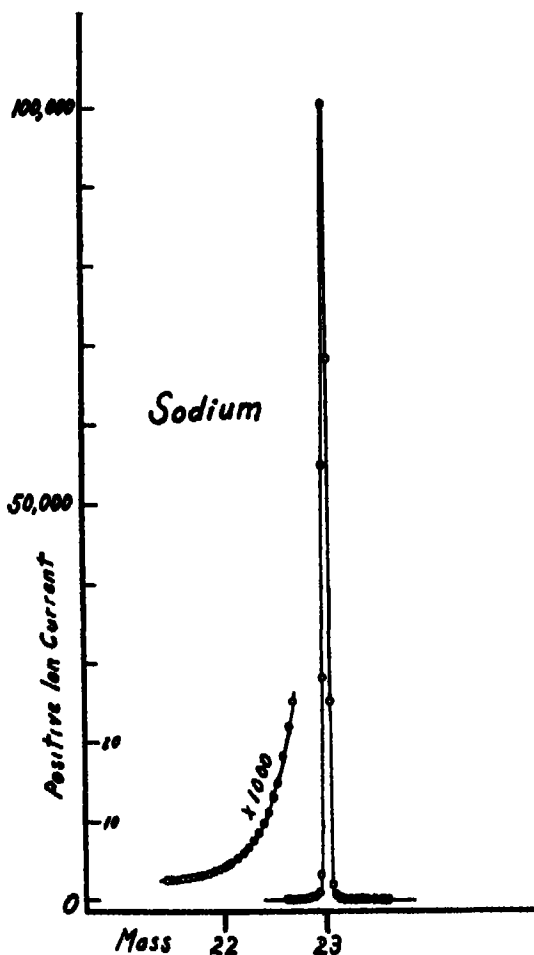


FIG 5 Positive rays of sodium. The region around mass 22 has been magnified 1000 times

these results with Brewer's unless one of us is mistaken on the relative abundance or the peaks which have been observed are spurious effects of some sort.

Cobalt.

Slow neutrons are absorbed rather strongly by cobalt, which is supposed to be a simple element, with the emission of γ -rays, but only a very weak activity has been reported to correspond with these facts.⁴ The indication was therefore strong that a new isotope was to be found either adjacent to the well known Co^{59} or if not adjacent, then two activities produced by slow neutrons might be observed. A search with the mass-spectrograph revealed⁹ some evidence for a new isotope Co^{57} when CoCl^+ ions were studied. Co^+ itself could not be used in this case because of an impurity which appeared at mass 57. The abundance ratio $\text{Co}^{59} : \text{Co}^{57}$ seemed to be about 600 : 1. A cylinder of cobalt was then subjected to bombardment by slow neutrons from a 68 mc. radium-beryllium source for nearly a month after which several days were allowed for any short period activity to die down. The cylinder was then found to be active, decaying very little over a period of several weeks. The active body has not yet been identified chemically nor has the effect been shown to be due to slow neutrons exclusively, however, the evidence combined with the information furnished by the mass-spectrograph, argues strongly for the existence of an isotope of cobalt of mass 57.

Beryllium

The question of the stability of Be^8 is an interesting one since this nucleus has been invoked to explain several nuclear transformations. Its existence in nature is questionable. A careful search was therefore undertaken with a mass-spectrograph.¹⁰ The metal was vaporized from an oven and ionized with slow electrons. A peak of Be^9 10,000 times as big as the smallest that could be detected was easily obtained but no trace of Be^8 could be found. This experiment establishes an upper limit of about 1 in 10,000 for the relative abundance of Be^8 in natural beryllium.

Strontium and Barium

An investigation of the strontium and barium ions emitted from hot filaments coated with the oxides of these elements revealed ¹¹ two hitherto undiscovered isotopes Sr^{84} and Ba^{134} as well as the ones previously reported by Aston ¹² Independently Dempster ¹³ found Ba^{134} and two others Ba^{132} and Ba^{130} . Since that time we have confirmed his discovery and measured the relative abundance of all the barium and strontium isotopes. The results are as follows:

Strontium	84	86	87	88
Per cent	0.5	9.6	7.5	82.4

Assuming a packing fraction from Aston's curve of -8.2 the chemical atomic weight as determined from these measurements is 87.62 in good agreement with the chemical value of 87.63.

Barium	130	132	134	135	136	137	138
Per cent	0.16	0.015	1.7	5.7	8.5	10.7	73.1

Assuming a packing fraction of -6.1 the calculated atomic weight is 137.35 which agrees satisfactorily with the chemical value 137.36. All of these values agree reasonably well with Aston's measurements.

Palladium, Iridium, and Platinum.

The isotopic analyses of palladium, iridium and platinum have been made by Dempster ¹⁴ but no measurements of relative abundances were reported. Using the ionized vapor source we have confirmed Dempster's results and have succeeded in getting reasonably good abundance data. No new isotopes were found.

For palladium we obtained the following data.

Palladium:	102	104	105	106	108	110
Per cent:	0.8	9.3	22.6	27.2	26.8	13.5

Using a packing fraction of -6 the value 106.6 is obtained for the atomic weight as compared to 106.7 for the chemical value. The mass spectrum is illustrated in figure 6.

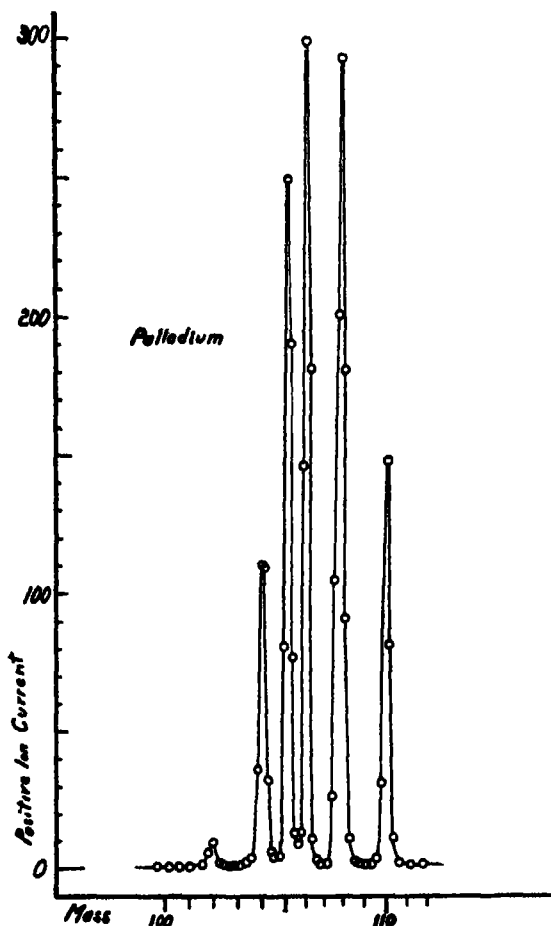


FIG 6 The relative abundance of palladium isotopes

The results in iridium are given below and the peaks are shown in figure 7.

Iridium·	191	193
Per cent.	38.5	61.5

Assuming a packing fraction of zero the atomic weight calculated from these data is 192.2, much lower than the chemical

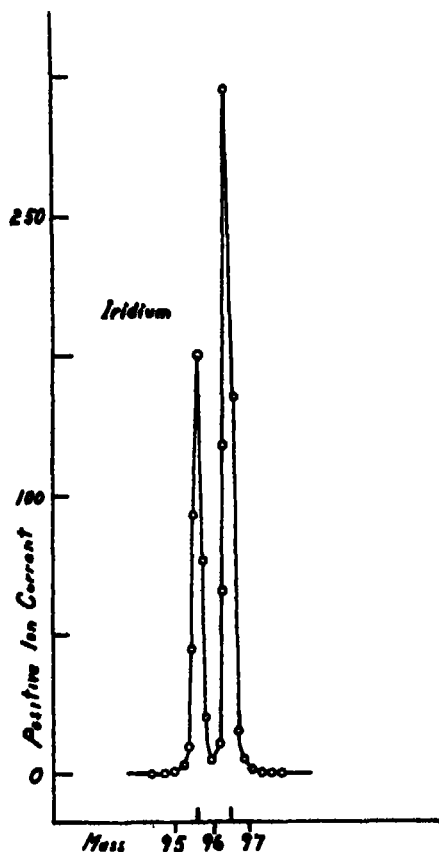


FIG 7 Second order mass-spectrum of the iridium isotopes

value 193.1. It seems probable that the chemical value is too high.

An analysis of the isotopes of platinum gave the relative abundances tabulated below.

Platinum.	192	194	195	196	198
Per cent.	0.8	30.2	35.2	26.6	7.2

Taking a packing fraction of $+0.5$ the calculated atomic weight is 195.12 in good agreement with the chemical value which is listed as 195.23.

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PRINCETON, N J,
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SOMATIC SEGREGATION IN RELATION TO ATYPICAL GROWTH

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(Read November 27, 1936)

ABSTRACT

Color changes during development have long been noted in plants and have been considered to result from somatic mutation and non-disjunction, deletion and other chromosome aberrations. In maize loss of color in the aleurone layer of the seeds has been found to be accompanied by an increase in color in adjoining cells. In these cases there has been a shift in such a way that a dominant gene has been removed from one daughter cell and doubled in the other. In these paired mosaics linked genes are sometimes shifted together and sometimes not. This indicates a process of somatic segregation that does not involve chromosome aberration.

These color changes are accompanied by growth changes which range from cells slightly larger than normal to depressions and outgrowths. Similar changes also occur in *Drosophila* as the result of somatic segregation.

GENETIC changes during development have long been noted in both plants and animals. The most frequently observed alteration is in color where the deviating tissue shows the expression of a recessive pigmentation. Nearly all heritable variations that result from germinal recombination, also appear sooner or later as somatic variations.

Color changes are easily seen in the aleurone layer of the mature maize kernel. This tissue is a single layer of cells surrounding the endosperm and underneath the pericarp which is maternal tissue. The aleurone cells are a part of the endosperm and are therefore 3n in chromosomal constitution and correspond in genetic composition to the embryo. When the seeds have the essential color genes present and are heterozygous for the aleurone color inhibitor which makes the seeds normally colorless, patches of colored cells are easily seen against a colorless background. These colored areas are irregular in outline and range in size from about half the surface of the seed down to single cells. The frequency of

these mosaic areas varies widely in different families, from none to more than one hundred in a single seed.

When the seeds are heterozygous for one of the complementary color genes colorless spots are seen on seeds that are otherwise red or purple. Frequently these colorless areas are accompanied by adjacent areas that are darker than normal. Both alterations usually have the same size and outline, one being a mirror image of the other. These paired mosaics, or twin spots, obviously result from one cell that during development has undergone a segregation process of some kind such that the dominant aleurone color gene is removed from one daughter cell and doubled in the other. Twin spots have been observed as the result of a similar shifting of several other genes in maize in both endosperm and pericarp tissue and in other plants. They have also been studied extensively in *Drosophila* by Stern (1936).

When the seeds showing paired color mosaics are also heterozygous for other genes on the same chromosome having visible effects on the endosperm it is noted that the colorless parts are sometimes recessive for the other linked genes and sometimes not. From all this evidence it is proved that the paired mosaics are not due to mutation, non-disjunction, deletion or translocation but are due to some process analogous to crossing over as Stern and others find in *Drosophila*. In plants no process is known, as yet, whereby homologous chromosomes may come together and effect this interchange.

Further investigations are needed to understand fully the mechanism of somatic segregation in plants. The important point is clear that there is a normal process of gene segregation operating in both plants and animals that is not dependent upon chromosome aberration as previously supposed.

While the two parts of a paired mosaic are usually equal in area they are not always so and this inequality extends all the way to single cells. Obviously some, at least, of the unpaired mosaics, colorless spots and dark spots along, start as twin spots but for one reason or another one of the two cells resulting from the segregation fails to develop or the subse-

quent growth is in such a direction that it does not reach the surface. Not all single mosaics can be accounted for in this way, however. The unpaired white spots are larger and more numerous than unpaired dark spots.

Many other changes have been noted in maize seeds such as large cells, giant cells, changes involving genes in different chromosomes, cell failures and cell outgrowths (Jones, 1935, 1936). Cell failures are manifested in pit and furrowed depressions lined with the remains of disintegrating cells. Apparently cell division has taken place but before maturity this tissue has broken down leaving a cavity underneath the unbroken pericarp. Any abnormal activity of these food storage cells might easily result in their failure to assume their normal firm structure and result in an unequal surface on the seed at maturity.

Cell outgrowths appear in many different forms. The endosperm tissue may be raised slightly above the surrounding area without breaking the pericarp. In other cases large spherical masses of cells rupture the pericarp and grow out in a distinct tumor-like structure. Depressions and outgrowths sometimes coincide with paired color changes, the colorless area being depressed and the darker area grown out, or the reverse. Paired depressions and outgrowths are also seen unaccompanied by any other change. Various kinds of growth changes alone or in combination are sometimes adjacent to color and other alterations where known genes are removed.

All of the evidence points to the conclusion that atypical growth results from somatic segregation whereby recessive genes, lethal genes, or chromatin derangements or losses are uncovered by the removal of their corresponding normal alleles in their homologous chromosomes. This segregation may result from chromosome aberration but not necessarily so since it has been shown in both animals and plants that segregation without loss of chromatin regularly occurs in somatic tissue.

A fasciated ear of maize has been found with a sterile sector

involving four rows of kernels at the base. As this ear grew the sterile sector became wider until at the tip it occupied nearly the entire ear. From the base to the tip the glumes, which are normally present as chaff at the attachment of each kernel, were forced into abnormal and freakish growth, becoming more extreme at the tip of the ear. This is a case where an abnormal sterile sector of tissue has grown at a faster rate than normal tissue and has forced normal structures into a freakish development. This is a growth mosaic that fulfils the specifications of a plant cancer.

The progeny grown from the seeds on the normal part of the ear in two generations has failed to give a return of a similar expression. Some of the plants have shown some irregularity in tissue development. When the seeds were examined for endosperm mosaics it was found that some of the progeny have an unusually high rate of mosaic formation. These mosaics take the form of giant cells, giant cells paired with colorless areas, giant cells darker than normal paired with red cells, colorless and red cells alone and paired with normal cells and with giant cells. In some cases this mosaic tissue is grown out beyond the normal tissue. The frequency of these mosaics is extremely high, ranging up to many thousands of alterations on a single seed. The original ear shows a similar high mosaic rate on some of the seeds.

Tumors and outgrowths have also been produced in *Drosophila* as the result of a recessive lethal factor (lethal-7) in the heterozygous condition released during development by the removal of its normal allele by somatic segregation (Jones, 1936). Wilson (1924) has reported an inherited benign tumor in *Drosophila* dependent upon several genes which must be in the heterozygous condition. The frequency of occurrence of these tumors varies considerably in different strains and with the vigor of the flies.

Tumors in animals and galls in plants are often the expression of a general abnormal growth stimulation apparently due to an increase in a diffusible growth stimulating substance. In some cases these abnormal growths reproduce

their abnormal condition when transplanted to another host or removed from their original site and allowed to regenerate. In these cases there must be a genetic change in the abnormal cells themselves.

In other cases the transplanted or regenerated abnormal tissue returns to normal. In this case, apparently, no permanent alteration in the nature of a genetic change has taken place in the deviating cells themselves. But a change of some kind has occurred in the host and where there is no indication of an external influence this change should be looked for in those parts of the organism that produce the growth stimulating substance. A genetic change in these tissues could be accounted for by somatic segregation. Additional evidence on this point is needed. It is significant that non-inherited fasciations in plants have their counterpart in variations that are inherited and propagated asexually.

Radiations of various kinds (radium, x-rays, ultra-violet light) are known to destroy or derange parts of chromosomes. In many cases the cells die. Only small injuries permit cell division. Nebel (1936) has shown that a small part of one strand of a chromosome may be affected as shown by achromatic spots. When these altered strands are transmitted to daughter cells the normal part in a homologous chromosome is capable of carrying on essential functions. But when this normal homolog is removed by somatic segregation or by chromosome aberration the resulting cells with homozygous or hemizygous defective chromosomes are no longer able to function normally. In many cases they are inviable but in others they have the ability to grow but in an abnormal and unregulated manner. This accounts both for the sporadic nature of atypical growth following radiation and its delayed manifestation. It also makes understandable the inability of these external agencies to do anything more than may occur spontaneously in the organism itself.

The minute bristle variations in *Drosophila* are known to be small chromosomal deletions that are viable only in the heterozygous condition. They also increase the frequency of

somatic crossing over. Radiations may, therefore, have at least two genetic effects on living organisms: they destroy essential growth regulating genes and also increase the chances that defective genes, whether induced or inherited, may be brought into homozygous expression and operation during development.

Somatic segregation whether due to normal crossing over or to aberrant chromosomal elimination makes understandable the sporadic nature of atypical growth with varying frequency in different families. Somatic segregation varies according to the condition of chromosome stability. This is known to be influenced by genic, cytoplasmic, and internal as well as external environmental conditions. Somatic segregation is increased in frequency by the same physical, chemical, and biological agencies that also increase the frequency of atypical growth in both animals and plants.

This is a preliminary summary of an investigation that is being carried on with the aid of a grant from the Penrose Fund of the American Philosophical Society and also from the International Cancer Research Foundation.

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TRAINS OF THOUGHT *

EDWARD L. THORNDIKE

THE sequences of ideas or trains of thought have interested psychology since its beginning, but have never been the subject of adequate investigation. Two methods are desirable in collecting extensive data. One is to have certain persons, whenever they find themselves in the course of a train of thought, stop and record it back to its beginning, or as far back as they can. The other is to give them some stimulus (call it A), ask them to say or record what thought A arouses (call this B) and then what they think of next, and so on for so long as the experimenter thinks desirable.

The former method is likely to secure more vital, full-fledged, "natural" and uncontrolled trains of thought, but omits many of the more evanescent, uninteresting, prosaic, and routine ones. It seems best to use it only as a check and supplement to the systematic experimental method.

The latter method may be operated in many ways. I have obtained trains of thought expressed always in words, have started the thinking on its course by a word, and have required the person to record the words just as they come, writing them in a column, until he has recorded forty. He then stops, does something else for a few moments, and then is started on another series by another word. For each of 65 persons, I have 100 such series of 40 words (or phrases), making 6500 words thought of in direct response to a given word, and 253,500 words thought of thereafter, 260,000 in all. These subjects of the experiments were educated adults, all accustomed to a wide variety of psychological experimentation. Four trial series to familiarize them with the task preceded the main experiments. The time schedule for these

* The investigations reported in this article were aided by a grant from the American Philosophical Society.

and the hundred words used to start the series, are shown in Table 1. There were 21 sessions, on 11 days, from 1 to 20 days apart, spread over a period of 40 days. Persons who

TABLE 1
SCHEDULE OF THE EXPERIMENTS *a* AND *b* DESIGNATE DIFFERENT SESSIONS
SEPARATED BY 3 HOURS OR MORE

Set, Initial word, Date	Set, Initial word, Date	Set, Initial word, Date
1 afraid 9, 6	35 fruit 9, 12 ^b	69. salt 9, 20 ^a
2 anger "	36 girl 9, 13 ^a	70. scissors "
3 baby "		71 sheep 9, 20 ^b
4 bath "	37 green "	72 short "
	38 hammer "	
5 beautiful 9, 7 ^a	39. hand "	73 sickness "
6. bed "	40 hard "	74. sleep "
7 bible "		75 slow "
8 butter "	41 head 9, 13 ^b	76 smooth 9, 21 ^a
	42 health "	
9 black 9, 7 ^b	43 heavy "	77 soft "
10 blossom "	44 high "	78 soldier "
11 blue "		79 sour "
12 boy "	45 house "	80 spider "
	46 hungry 9, 14 ^a	
13 bread "	47 joy "	81 square 9, 21 ^b
14 butter "	48 justice "	82 stem "
15 butterfly 9, 7 ^c		83 stomach "
16 cabbage "	49 king "	84 stove "
	50 lamp "	
17 carpet "	51 light 9, 14 ^b	85 street "
18 chair "	52 lion "	86 sweet 10, 11 ^a
19 cheese "		87 swift "
20 child 9, 7 ^d	53 long "	88 table "
	54. loud "	
21 citizen "	55 man "	89 bitter "
22 city "	56 memory 9, 18 ^a	90 tobacco "
23 cold "		91 thief 10, 11 ^b
24. comfort "	57 music "	92 moon "
	58 mountain "	
25 command "	59 mutton "	93 whiskey "
26 cottage 9, 12 ^a	60. trouble "	94. whistle 10, 12
27 dark "		95 white "
28 deep "	61 needle 9, 18 ^b	96. window 10, 16
	62 ocean "	
29. doctor "	63. priest "	97 wish "
30 dream "	64 quiet "	98 working "
31 eagle 9, 12 ^b		99 woman "
32 earth "	65 red "	100. yellow "
	66. religion 9, 20 ^a	
33 eating "	67. river "	
34. foot "	68. rough "	

were unable to keep any of these appointments attended special sessions to complete their quotas.

THE CAUSATION OF TRAINS OF THOUGHT

The first question of importance concerns the extent to which these trains of words or thoughts expressed in words are explainable by chance. If all the words which a given person knows and could write were written on cards, shuffled in a bag, and if 4000 were drawn from the bag at random (each being put back before a new drawing) and arranged in series as drawn, how far would the results be similar to those obtained from the experiments. A casual and superficial inspection of parts of the latter may give the impression that mere chance is predominant often, but this is false. It is true that sequences sometimes appear which are neither logical nor habitual, and which could not be predicted with more than one success in several thousand. Such apparently chance sequences in the train of thought may appear as a result of loss in zest for the activity. The consequent failure of any word to be called to mind by the preceding words leads the person to search about for any word. "Write a word—any word" or something to that effect, is in the background as a part of the general mental set or adjustment, and evokes such search when the sequence of particular words fails to continue itself fluently. Prediction of which word the search will bring forth in such cases will not have many successes, though it will be well above chance, there being a strong tendency in such cases to call up the name of some very common object or quality. Discreditable ideas may occasionally be omitted from the record, and such omissions may produce the appearance of chance sequences.

A simple and satisfactory measure of the difference between trains of words thought of and trains of words drawn from a person's repertory by chance is obtained by observing how frequently a word occurring two times in the 4000 written by the person has in both cases the same word as its immediate sequent after allowance for those cases where the

word was the fortieth and so had no immediate sequent.¹ When a word occurs three times (I, II, and III) we treat it as equal to the occurrence of three pairs (I and II, I and III, and II and III). When a word occurs four times, we treat it as equal to the occurrence of six pairs (I and II, I and III, I and IV, II and III, II and IV, and III and IV). Similarly for words occurring five, six, seven, or more times. We thus construct a table like Table 2 for each person. In the case

TABLE 2

A SAMPLE CENSUS OF THE FREQUENCY WITH WHICH A WORD THAT OCCURS TWO OR MORE TIMES IN POSITIONS 1 TO 39 OF THE 100 TRAINS OF THOUGHT HAS THE SAME IMMEDIATE SEQUENT SUBJECT Cu

Occurrence	Frequency	Number having the same sequent			Total number of pairs having the same sequent	Total number of pairs which could possibly have the same sequent
		2 cases	3 cases	4 cases		
2	296	17			17	296
3	142	31	3		40	426
4	67	12	3	1	27	402
5	38	11	3		20	380
6	41	13	9		40	615
7	30	14	4	1	32	630
8	17	7	5		22	476
9	6	4	1		7	216
10	5	1	1		5	225
11	0	0	0		0	
12	1	0	1		3	66
13	2	1	1		5	156
14	0	0	0			
15	2	1			8	210
16	2	2			2	240
Sum					228	4338

of the person (Cu) whose record is shown in Table 2, there were 296 words occurring twice, in 17 of them the word had the same sequent both times. There were 142 words oc-

¹ Plurals in s and verb forms in -s, -ing, and -ed were treated as the same word as the primary form, both in finding the words occurring two or more times and in comparing their sequents

curring three times, affording 426 pairs, in 40 of which the word had the same sequent. There were 67 words occurring four times, affording 402 pairs, in 27 of which the word had the same sequent both times, and so on. In all, there were 4338 chances for the same word to have the same sequent at two occurrences, and in 228 of these it did.

In how many cases would two occurrences of the same word have the same sequent in a series obtained by chance drawings from Cu's repertory of words. We do not know the size of Cu's repertory, but we do know that, including names of persons, places, books, etc., it was well over 40,000¹. Cu is a college graduate aged about 35 who has read widely. His CAVD score (a score in intelligence operating with words and numbers) is 425, or well above the level of the average college graduate. He would know over 30,000 of the words listed in an English dictionary, and, in addition, many words in certain foreign languages, many names of persons, places, books, etc. not listed in the dictionary, the -er and -est forms of many adjectives (which by our rules counted as different words). Consequently if he should spend time and thought enough, as by starting with aa, aba, abb, abd, abe, abh, abi, and filling out as many as he could of each, he could have made a list of over 40,000. Two occurrences of the same word will then have the same sequent in random drawings from Cu's repertory less than once in 1,600,000,000 times. In our experiment Cu showed such occurrence over eighty million times as often as in chance draws from his repertory¹.

For nine other persons for whom the actual frequency was found from the data, and the frequency obtainable by chance was computed from conservative estimates of their repertories of words, the corresponding figures ranged from twelve million times chance expectation to two hundred million times chance expectation, averaging fifty-seven million times chance expectation.

In certain persons whose trains of words often take the forms of narrative or semi-narrative, statements of facts in

¹ Not counting plurals or -s, -ing, and -ed forms of verbs

sentences, and quotations, the frequencies would be disturbed by certain words which have occurred with so many different sequents in the course of life that they do not tend strongly to evoke any one of these rather than any other (such as *has, have, the, will, he, she, it*, etc.) These latter reduce the number of identical sequents to identical words. There are several such persons among our 65 men and women. But I have found no person whose records could by any conceivable stretch of possibilities be explained by chance.

The word chance is in fact much misused in connection with the mind. When a person says that an idea came to him by chance he is wrong. If I ask you to choose five animals quickly by chance from the animals you know, or to say at random a hundred of the words you know, one per second, I am asking impossibilities. The mind does not and cannot act at random. It would require elaborate precautions and much time for anyone to make an absolutely chance selection from the names of animals known to him, and he could not make a random selection of a hundred words from those he knew, save by marking all he knew in a dictionary and adding a list of words known by him but not in the dictionary!

What is, by error or by inadvertence, attributed to chance in mental life is commonly due not to chance at all, but chiefly to the enormous number and extremely complex interrelations of the causes involved. Not only can one prudently expect on general grounds that the mind is as truly determined as any living thing, one can find by observation and experiment that what seems most fortuitous in it is often a brilliant example of natural causation, but by a multiplicity of factors.

Trains of words thought of are caused, in my opinion one hundred percent caused, but they show few oft-recurring regularities of the sort commonly called mechanical. In the case of Cu the only words occurring three times or more which had the same sequents at every occurrence were cup, saucer (3 out of 3), buy sell (3 out of 3) knife fork (4 out of 4) sun moon (3 out of 3).

In the case of the other nine records especially studied, the

only such cases were: Benedictine monks (3 out of 3); Bronson Alcott Brook Farm (3 out of 3); gold silver (3 out of 3), cow pasture or pastures (3 out of 3), adjective adverb (3 out of 3), Madame Bovary Flaubert (3 out of 3); Marat Charlotte Corday (3 out of 3), monks monastery (3 out of 3), minutes seconds (3 out of 3), young old (3 out of 3), sister brother (4 out of 4), painting color or coloring (4 out of 4)

There would probably have been more such in trains of thought occurring in every-day life. In the experiments there may well be a tendency to avoid, or shift from, the obviously commonplace. However, the flow of ideas or words is rarely due to a few established routines. It is due to mental habits, past connections in experience and thought, but there are so many millions of these, facilitating, interfering, cooperating and competing with one another in so many ways, that routine is a very poor term to describe its nature.

There is of course plenty of regularity in the mind. Many of us think 17 whenever we are asked "How much is $9 + 8$?" with a regularity somewhat comparable to the movements of the planets. But most of this regularity is earned by careful repetition and reward, and maintained by strenuous protection of the mental connections in question from outside interference. Such associations, we say, are "controlled." Let these interferences have full swing and "how much is $9 + 8$?" may evoke "What do you want to know," "Do not bother me," "Find out for yourself," or even, " $9 + 8$," " $9 + 8$," "ate a tate." In the experiments, thought is left free, except for the task of thinking of and writing a series of words. Being thus free, it usually eschews dutiful thought. Very rarely does a person thinking "man" or "boy" or "he" continue with the plural "men," "boys," or "they." "Go" does not evoke "went, gone" as in a grammar class. Regularities employed to meet questions, fulfill intellectual duties, and attain practical ends are not called into action when the mind is invited to wander where it listeth and to do, within limits, what the words seen and written may in and of themselves suggest. It then lets its multifarious mechanisms or forces

connecting verbal responses interplay with only the degree of overhead control mentioned above. Words stream forth, in a series, every item of which is caused, but few items of which are in habitual routine

The complexity of mental causation may be realized by observing the variety of sequents of words which occur eight times or more within the four thousand Table 3 presents

TABLE 3
SEQUENTS OF WORDS OCCURRING EIGHT TIMES OR MORE IN THE RECORDS OF
AV, BAU, CUR, F D, AND FRU

Person	Word	Sequents
Av	<i>beautiful</i>	happiness pretty gaudy dirty character wile-y cobwebby study Chinese pane
Bau	<i>black</i>	skin race ball flag (2) terror foreboding Wotan abyss list
Cur	<i>art</i>	artists exhibit museum (2) landscape architecture
	<i>arts</i>	fine arts literature
	<i>book</i>	cash library parodies
	<i>books</i>	learn shelves study college newspaper (2) dresser faculty library
F D	<i>blue</i>	flag white (2) hurrah squares bright waves blues violet Shaw
	<i>air</i>	sunshine (2) open sun cottage ceiling seashore camp bed
	<i>ball</i>	park ship bread stone catcher game crowd wade
	<i>balls</i>	airplanes
	<i>blue</i>	waves song color complexion fish water (2) ribbon catch sea
	<i>boat</i>	ocean sail (2) sailing can cut ride water captain
	<i>book</i>	black literature write play soil draw picture novel mother lights flag paper read place novel magazine sing newspapers clothes shelf library write short radio fool books piece shelf thread draw powder place food
	<i>books</i>	play (4) mother cut orchestra ball fat four siren
	<i>box</i>	girl flowers flying sunshine moisture invigorating breathe sunlight shut
Fru	<i>boy</i>	red roses assurance night floor cot sinking cases chair
	<i>air</i>	fight healthy flying night long legs polish contrast
	<i>bed</i>	trees green (2) colors pale delightful clouds rolling piers
	<i>black</i>	magazine (2) holy list public
	<i>blue</i>	looks teacher print understanding hang meals ends friends
	<i>book</i>	
	<i>books</i>	

the facts for words in A and B for five persons. They show no mixture of mechanical routines with chance concatenations, but the subtle, disorderly sort of orderliness which is characteristic of the mind

For the purpose of proving that the trains of free thought of our records are never caused by chance nor, on the other

hand, often caused by fixed routines, I have used the relation between a single word and its immediate sequent. But it would be absurd to assume that such thinking proceeds in units of one word at a time, or that the determination of a person's thought at any point in such a train is chiefly by the single word he has just written or the single idea which he has had acting upon him, i.e. upon his total nature or equipment. He is at that moment also under stimulation by the preceding thoughts in the train, by relics of the printed word which started it, and by concurrent circumstances.

There is a range of causation from cases where the last single word or idea is very prepotent to cases where it weighs very little in comparison with the influences from the primary stimulus and train to date. Clear cases of the former are where the mere sound of a word calls up a word of similar sound as in *pray play*, or *reed feed*, or *blackboard blackmail*. Cases of the latter occur often in this train started by the printed word *butter*. "yellow soft fat water adulterated coloring calories 1000 p. lb. food nourishment bread cooking dishes eggs frying sizzling frying-pan flows gravy piquant unhealthy diet bread living struggle inconsiderate forced justified perversity social morale production cows milk cream buttermilk ice restaurant squares salty."

Cases where concurrent circumstances determine the course of thought may be illustrated by the writing of *amen* when the fortieth line of the record sheet is reached.

A more detailed study of the sequences of thoughts with consideration of all these influences at work would strengthen the case against chance on the one hand and against a few millions of simple routines on the other. The examination of the records by any competent person by any reasonable method will, I am convinced, support the conclusion that the writing of every one of these thousands of words by the persons was as truly determined by natural causes as was the digestion of their food, or their metabolism and growth, but that the determining forces are very complex.

THE FORCES OPERATING IN THE FREE ASSOCIATION EXPERIMENTS

Orthodox psychology has contrasted free association sharply with controlled association. In the former, ideas are supposed to suggest one another for no purpose and with no direction from outside themselves; in the latter, the process is stimulated and guided by some purpose which largely determines what ideas any ideas shall suggest and which of them shall be welcomed, given attention, and selected to influence further thought. Free association is supposed to be a rather automatic play in which the mind naturally indulges when duty does not call it to serious purposive thinking, and to be the normal direction of the current of the stream of thought from which certain intellectual demands divert it and to which it tends to revert.

This is all true, but it is not the whole truth. It does not give an adequate description of associative thinking nor of the difference between it and purposive thinking. It fails in three respects. (1) Association free from control by some aim, purpose or problem does not always equal a strictly "free" play of ideas; it is not free from control by past mental connections. (2) The chief actual alternative to purposive and selective thinking is not fancy or day-dreaming or utterly aimless mental drift, but habitual thinking. (3) Habitual thinking is not distinguished sharply from purposive and selective thinking by the total absence of purposes and guidance, but gradually by their relative infrequency. Almost all thinking is done with some purpose, but in thinking where habits are much more prominent than inferences the purpose may be a rather silent partner interfering in the process only occasionally and unobtrusively.

When in our experiments thought is freed from any requirements save that the person think of something reportable in words, the results show not only aimless drift and streams of fancy, but also revivals of past experiences and rational thoughts. Still more frequently there appear series of words which cannot be classified as fancies, or as memories,

or as reasonable thoughts, but are blends of two or all of these.

For example, Mr. Ef. approximates the typical freedom of fancy in·

- (1) "hot drink cognac cold weather snow winter fur restaurant dance enjoy royal officers capitalists religion"
- (2) "boy scout small uniform Baden-Powell South Africa war Boers Holland"
- (3) "garden Eden paradise bible study school geography Russia Leningrad."

He approximates the typical autobiography of memory in

- (1) "blue sky beautiful Ukrainia fields great peasant poetry Kiev South Dneiper river nice girls dance"
- (2) "father mother hotel trip mountains enjoy"
- (3) "school boys tough rough educated teachers dislike much transfer city different enjoy good school"
- (4) "restaurant second Avenue inexpensive music dance orchestra"
- (5) "friend visit often enjoy many functions bridge party people drinks radio dance all night morning go tired"
- (6) "dance eat drink go home subway sleep night all sunburn"

He attains or approximates the typical rationality of deliberate thought in·

- (1) *woman* "when one hears the word woman one may think of all kinds of women. One may think of his mother sister wife mistress etc"
- (2) *whiskey* "should be aged in barrels made of special kind of wood. Lot of cheap whiskey sold at present in United States is aged only few months"
- (3) *slow* "but sure. Some people in our group are very slow. It takes them nearly an hour to write up five strips of paper. But it takes me only about ten minutes. It is much easier to write a story Amen"

He shows the blend of forces ordinarily operating in the brain in our experiments in·

- (1) *bible*: "Sunday school lesson preacher boys seminary Fosdick chapel modernistic progressive reactionary

orthodox Episcopalian Methodist Luther evangelical
missions priests Africa Mohammed Islam Christianity
Jews Talmud Dr. Wise popularity persecution Hitler
humanity emigration liberty freedom U S. A. K.
K. K."

- (2) *child* "play many family marriage prevent babies birth-control doctor visit Mrs Sanger idea new control enjoy life poor family often miserable religion prohibit priest church teaching progress Soviets Russia babies enjoy family play population decrease France much nation soldier defend war killed."

As a corollary of the facts of this section, one may note that "free" association of ideas in the sense of just letting ideas come into one's mind is by no means a natural play and enjoyable relief for all persons. If the instructions had been to "Write 40 numbers," "Write 40 names of animals or plants," "Write 40 words beginning with a," "Write 40 given names," "Write 20 pairs of opposites like *good bad*," "Write 10 questions of 5 words each," and such like, the experiment would have required *less* time and *less* effort from many of our group.

THE MENTAL CONTENT IN TRAINS OF THOUGHT

Thinking of Realities and Thinking of Words

A person who is asked to look at a stimulus word and write the words that come to his mind until he has written forty, may think of things (including persons and animals), qualities, acts, feelings, events, facts, questions, commands, etc., and write words expressing or suggested by the things, qualities, etc., which he thinks of. Such primacy of realities was presumably the case in the following:

Thoughts of Things

- (1) "camp pine-tree cabin lake"
- (2) "Tahiti Gauguin deserter leprosy."

Thoughts of Qualities.

- (1) "Aztec design rug gray black red"
- (2) "brown soft eyes sweet quiet serene."

Thoughts of Acts.

- (1) "wave flag cry shout"
- (2) "look laugh admire ask talk."

Thoughts of Feelings.

- (1) "glad gay happy laughter"
- (2) "worry anger resentment hatred "

Thoughts of Events.

- (1) "dentist drill a hole bore down deep hurt."

Thoughts of Facts.

- (1) "art is fleeting time never stops"
- (2) "this proves conclusively that all is not well with me"
- (3) "hand rocks cradle rules world."

He may think of words with little or no thought of their meanings, or with thoughts of their meanings as sequent and secondary to the thoughts of the words themselves. Such primacy and dominance of the words was presumably the case in most of the following

- "rake rash radish"
- "small smell snake"
- "concern yourself yearn yet yoo-hoo"
- "week-end weaken"
- "Shakespeare peer"
- "Curie cure "

These two sorts of thinking may and often do occur alternately or together, and combine in influence. Thinking of words as sounds or sights may intrude and for a time predominate in series which consists chiefly of thoughts of meanings as in "Hark Hark lark Larkin," or in "hard boiled bake muffin muffed tuffet." Thinking of the meaning of a word may intrude in a series which is chiefly verbal as in "weak willing wager wage war wilt" or in "money moon merry month May maggot." The two sorts may coact subtly as in "weird willowy wasp waist" or in "wait whisper waken at night wonder why world want wage war against war."

"Focal" or "Substantive" and "Fringe" or "Transitive" Thoughts.

In many forms of experiments on thinking there is a tendency not to report the relational "fringes" of thought—the thoughts of *at, in, of, to, and, but, or, is, was, can, who, that,* and the like. The subject often does not notice them, or does not consider them worthy of record. And this was doubtless true of many of our adults. However, they could fill out their lists of forty words more quickly by including the words which carried these fringes of relation and some of them often did so. When they are reported as parts of very free, happy-go-lucky trains of thought, the results are interesting. I quote some samples

- (1) "seek years strive never reach nor be disillusioned for one cannot realize and accept without disappointment but reconcile concede concession Coney Island"
- (2) "fodder for horses and pasturage in arid Arizona where sun shines (but + all + is) dry why (no + one + knows) drought nought suffices (we + must + go) sooner or later too Heaven forbid such atrocities beware the dog now listen"¹
- (3) "light shine greenly up above never love nor leave never grieve nor a sieve for rice to saunter through slowly starchily whitely and brightly"
- (4) "never divide by two because it's wicked and besides nevertheless I (do + not) know nor care nor (can + ever) believe myself"

Such irrational use of relational words in the thoughts by an entirely sane and able intellect may offer useful comparisons with the uses of relational words in the thoughts of the insane and hysterical, and in certain writings of Gertrude Stein and others.

¹ The parentheses and plus signs here and later mean that the person wrote the two or more words on one line so that the set in question had more than ~~20~~ words

FORCES OPERATIVE IN EXPERIMENTAL TRAINS
OF THOUGHT

The stimulus word rarely exhausts its influence when it has evoked thought producing the first word written. It usually acts somewhat in the determination of the later thoughts and writing. So clearly in *bed*: "lie make get up," *butter* "bread yellow soft melt," *cabbage* "baggage patch," *chair* "camp stool," *citizen*: "ship of the world," and *comfort*: "warm cosy tea-kettle," from the first quarter of Be's records. It may exert a demonstrable influence far along in the series, as in *music*: "classical modern listen over many times Beethoven Brahms Bach three composers like best of all include in list other musicians orchestra Philharmonic symphony ninth choral chorus ode to Joy Schiller German Hitler race . ." Some persons exaggerate this tendency into a system, keep the stimulus word emphatically in mind, and write forty words all of which are determined largely by it, as shown by the words of Wo in the series started by *afraid* and *baby*

afraid "fear dark storm burglars danger policeman fight lightning war hatred malice night poverty future enemies guns knives hold-ups beasts forests wild undertow tides cyclone earthquakes fires frightened dreams insanity mob communism death overeating flat-feet obesity indigestion heart failure arsenic gangsters"

baby "cute pink round mother milk diapers cap dresses ribbons carriage nurse mammy crying noise colic first tooth floor walking sleeplessness medicine doctors neighbors complaints callers rattler teeth presents bath play kitten powder crawling crowing first word paregoric pills pains stomach-ache"

Similarly any thought or word that comes to mind in the course of the train may continue to exert an influence after its immediate sequent has been evoked.

What word shall be written at any given point in a series

may thus depend on all that have been written so far. It may also depend upon the set of the mind of the writer at that day and hour, and upon the knowledge, interests and attitudes which are characteristic of his enduring personality or make-up

On the other hand, a small fragment or minor feature or special aspect of a word or words may nearly or quite monopolize the entire causation of thought. So, for example, in "conglomerate gloom" (nothing in the series preceding *conglomerate* has any conceivable fitness to evoke gloom, and nothing in conglomerate itself except the *glo*). The same is true of "Shakespeare peer."

We have noted the fact that entirely free uncontrolled wandering of thought is the exception rather than the rule. Most persons never show it and it is rare even in those who do. As nearly pure cases of it as I have found are the following from Be

eagle "eye hawk hook needle camel hump back cripple Notre Dame cathedral chair chaise longue French pink green alabaster lamp ebony jade studded exemplify attitude poise awe reverence veneration devotion idol ideal church religion crisis who Nemesis my fate destiny hands maker"

whistle. "pop goes the weasel wow whoopee crazee soultee (?) tame the easels of artists deluded show the master's nature's concluded when dog eats dog and man robs man and this proves conclusively that all + is not + well with me but why + should it be + Huh?"

The rule is that a person adopts habits or systems which more or less direct his thought. The commonest of the systems or sets of mind which thus operate as directive and selective forces is to think of things that reasonably go together. So Be's record shows *earth* "round ball top spin," *foot*: "hold grip ground jump off place lover's leap precipice cliff," *hammer*: "away toward shoemaker cobbler nail shoe," and *health* "clinic nurse doctor eyes strabismus myopia."

It is not very unnatural or hard for these minds to do this. On the contrary, it is precisely what they have been doing in most of their thinking for twenty years or more. What would come to mind even without any direction or selection would often be a reasonable thing or fact to think of, and a little care to think of something fitting may actually increase one's ease and comfort in the experiments. There need be nothing dishonest, artificial, pedantic or strained in such trains as these

- (1) "window evening-star Wagner music Chopin Liszt"
- (2) "monk anchorite hermitage retreat sequestered secluded"
- (3) "parapet ruin Athens white marble columns ivy acanthus Corinthian"

In fact, they and much more erudite ones are from the same person who wrote the *whistle* series above, and were as natural sequences for her as it was

Other common systems are to think of things that belong together in space or events in time, or words that rhyme, or words that are alliterative, or words that end in *-ing*, or familiar quotations. All of these are very frequent in our records (though some persons manifest none of them). In the case of writing words that begin with the same or similar sounds or end with the same or similar sounds, there is often, as noted earlier, a considerable cooperative force from meanings, some of the words are likely to be such as might have been called up for reasons of meaning alone. Such is the case, for example, with (1) "swim sink save saunter lane lake lyre", (2) "partner pageant people pillory part", (3) "come creep crawl crouch cringe"; and (4) "mouse louse spouse souse."

Reminiscence and autobiography, which occur occasionally in the trains of thought of all the persons, may be exaggerated into a prevalent system by some. So we have, for example,

needle. "this word amuses me it is (illegible) being a poor sewing pupil I evolved into a teacher of sewing in

occupational work and kindergarten work I suppose there is such a thing as a (illegible) because the work was (illegible)"

stomach "ache last night ate too much therefore bad indigestion acute sharp keen pain right side low "

There may also be special systems adopted more or less frequently. One of our group used very often a sort of commonplace and elementary didactics. A sample is. *stove*. "cook your food on this thing fire is very low a good cook always keep this in mind that it is most important to turn the flame on if you want your victuals to be ready in time don't forget "

Another wrote many personal reflections, sometimes in a genuine, sometimes in a mock, literary vein, such as.

bible "for centuries called the good the only book fit to read yet a bit of fair-minded reflection shows"

comfort "and cosiness Yes that's a pretty picture to contemplate a nice cosy fire books and on the table near you a bottle of port and a stack of books outside perfect silence inside perfect peace sip read you're in clover"

butterfly "on a summer's afternoon where the honey-suckles bloom and old nature's at the best there I beheld I guess beheld is the proper word ain't it. There I beheld a butterfly a swallow-tail it was winging its way to bliss "

The desire for pleasant or even voluptuous imaginations which operates is much day-dreaming is not apparent as a cause of what is written, and probably did not cause much that was thought but not written¹. Thinking to order and filling up columns with the words thought of is not suggestive of, or conducive to, dreams of love, wealth, power, and glory. In a thousand sets which I read, there was not one clear case

¹ Some of our persons were extremely frank in references to the indulgence of animal appetites, but they showed little or no more evidence of directing the trains of thought toward pleasurable imaginations than the others

of a daydream of that sort, though one person intimated that what she wrote was not what she was really thinking about. Reminiscences of past pleasures were fairly common but imaginations of future ones were certainly very rarely, if ever, systematically sought in the experiments

The forces determining what is written in these continuous series of forty words are on the whole much more varied and complex than those determining what is written or said in single responses to stimulus words. In the latter case, about ninety-five percent of the responses are due to connections formed with the stimulus words in hearing and reading, and in speaking and writing. They reveal chiefly what the individual has heard, read, said and written, weighted by his interest therein, and what connections have operated to give meaning to words heard and seen.

The facts may be illustrated by the words *yours*, *good*, *cold*, *ja*, and *bed*. One of these words may (1) evoke some word which has been a frequent and satisfying accompaniment or sequent belonging to it in speech or writing, as in *yours truly*, *good morning*, *cold weather*, or *bedclothes*. It may (2) evoke some word which has been a frequent and satisfying accompaniment or sequent, belonging to it in hearing or reading and helping to give it meaning, as in *yours mine*, *good bad*, *good nice*, *cold Alaska*, *cold frigid*, *cold hot*, *ja yes*, *bed sleep*. It may (2a) evoke some non-verbal representation, which has been a past accompaniment of the word, of some thing or quality or event which helps to give meaning to the word. The subject may then write a word which names this nonverbal representation or is suggested by it. So we may have *cold* arousing wintry images and so the words *snow ice*. It may (2b) evoke some tendency which has functions like those just described but is non-representative, which tendency leads the subject to write its name or some word suggested by it. So *cold* may produce *b-r-r-r-r*. (3) The stimulus word may set in operation other connections than these of use and comprehension. So with *cold mold*, *cold pain*, and *cold yesterday*. I find the proportions of cases

to be about 20 of (1), 75 of (2), and 5 or less of (3).¹ These estimates are derived from a detailed study of records obtained by myself from 162 or 192 educated adults, and of the records from 1000 children furnished by Woodrow and Lowell ('17) and from a less careful study of the records of Kent and Rosanoff ('27), and O'Connor ('28) ²

In the serial associations the percentage of Class 2 is much reduced, and the associations of Class 1 are much altered by the cooperation of other forces

CHANGES IN THE MODES OF THINKING IN THE COURSE OF THE EXPERIMENT

The number of sentences including quotations increases greatly during the course of the experiment. Of fifty persons in whose records this matter was examined, four showed a very slight drop from Sets 1 to 4 to Sets 97 to 100, nineteen showed no change, and twenty-seven showed increase. On the average there are five times as many words in sentences and quotations in sets 97 to 100 as in sets 1 to 4 (11 to 2 per set of 40)

The number of rhyming and alliterative sequences also increases. Only one person shows a marked decrease ($2\frac{1}{2}$ per 40 to zero); four persons show marked increases (from zero or near zero to 9 per 40), ten persons show slight changes up or down, thirty-five do not use such sequences either at the beginning or the end of the hundred sets. The average number per 40 rises from about 0.15 to 0.80.

The writing of a sequence of species of some genus also increases to 1.1 per 40 during the experiment, roughly from 0.5 per 40.

These changes are probably caused partly by deliberate adoption of modes of thinking and writing found by one's

¹ The argument is presented more fully and with evidence in Chapter 14 of *The Fundamentals of Learning* (Thorndike, '32). Its starting-point was an investigation of the frequency of opposites among the responses. The connections of meaning explain that mystery and others.

² H. Woodrow and F. Lowell, *Children's Association Frequency Tables*. Psychological Monographs, vol. 22, No. 97. A. J. Rosanoff, *Manual of Psychiatry* (sixth edition), pp. 546-620. Johnson O'Connor, *Born that Way*.

own experience or reported by others to be pleasanter than the ordinary thinking of one thing, quality, act, etc. after another, and partly by inadvertent adoption of such. In one way or another two-thirds of the group learn in the course of the experiment to relieve its labor and monotony thus

INDIVIDUAL DIFFERENCES

Taking the records at their face value, the individuals differed greatly in what they thought about, in the predominance of reality versus verballity, in the systems operating to direct thought,—in fact, in well-nigh everything save the fundamental fact that associative links and readinesses due to past experience and present adjustments caused the observed behavior. For example, some persons write words about music ten times as often as some other persons (130 to 13). Much the same is true of words about art, or about language, or about religion, or about animals, or the use of *I*, *me*, and *myself*. The number of words referring to foods or eating varied from 53 to 193 (or perhaps still more widely, since this count was made for only half the group). Some persons never show rhyming associations, others have them in almost every set of forty. Some persons almost never write a sentence, others seldom write a series of disconnected words. Some follow some one system exclusively, others are very versatile and changeable. Some reminisce often, some almost never.

It would, however, be unsafe to assume that these differences truly represented all the trains of thought of the persons in question, much less their total thinking. A person may for one or another reason use a very restricted part of his total nature and repertory in an experiment such as this one. Four thousand words is enough to sample a person in this sort of thinking, but one sort of method is not enough. Several should be used, each independent of the others and all together representing an adequately weighted sampling of their thinking to be investigated, if inferences are to be drawn concerning individuals. A person whose mind was

set in this experiment toward dignified thoughts, and wrote after *Music* Toscanini La Scala Caruso Pagliacci clown He + Who + Gets + Slapped Andreyev Sabine + Women David Louvre Venus + de + Milo Apollo Belvedere Praxiteles, might in another experiment be set toward satisfying the requirements quickly or toward personal reminiscence, with a reduced score for art and music and an increased score for foods and common activities. The mere idea of using rhyming associations, or of thinking of words before thinking of their meanings may not have occurred to some of our group. If it had occurred to them, they might have used it systematically, or at least occasionally. During the progress of the experiment there was a notable increase in the use of quotations and sentences expressing facts (and also questions and commands). A person might shift from none of this to much of it simply from hearing from some friend that it was an easy way to get the columns filled. His general patterns of serial association would, however, be altered only infinitesimally by this bit of information.

TRAINS OF THOUGHT AS EVIDENCE OF PERSONAL TRAITS

What things a person thinks of and what he thinks about them are obviously important symptoms of his nature. How closely what he writes in such an experiment as this represents his ordinary thinking and so indicates his character and interests is, however, a matter for investigation. The facts will be made the topic of a later report.

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TRAINS OF THOUGHT AS SYMPTOMS OF INTERESTS AND ATTITUDES: AN EXPLORATORY INVESTIGATION *

EDWARD L. THORNDIKE

Each of sixty-five adults, mostly of intellect and education much above the average, wrote one hundred sets of forty words. The stimulus starting each set was a word (such as *afraid* or *angry* or *baby* or *bath*) and the persons were asked to write the words that came into their minds until the forty spaces on the sheet provided were filled. The experiment was spread over a month, five sets usually being written on any one day. The starting stimuli were the words of the Kent-Rosanoff list.

Various features of such written lists are presumably indicative of the natures of their authors to some extent and in certain respects. It is the purpose of this report to present facts concerning the indications furnished by the words which appear in the lists, regardless of their particular contexts.

Suppose, for example, that we count for each person the number of occurrences in his 4000 words of the following common words: ballad, banjo, bass, bugle, carol, Caruso, chant, chime, choir, chord, chorus, clang, concert, cymbal, discord, discordant, flute, guitar, etc., etc., and of such words outside the commonest 10,000 as: *adagio*, *Aida*, *allegro*, *alto*, *Amati*, *andante*, *anthem*, *aria*, *baby grand*, *Bach*, *bassoon*, *baton*, *Bayreuth*, *Beethoven*, *Bori*, *Brahms*. What correlation is there between this number and his interest in music as measured by some reasonable criterion?

Or suppose that we count the occurrence for each person of the following and check the results against some criterion of his interest in the church and religion: altar, baptism,

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Baptist, baptize, bible, blaspheme, blasphemy, censor, chapel, Christ, Christianity, church, churchman, clergy, clergyman, cloister, divinity, God, etc., etc. archimandrite, asceticism, atheism, Ave Maria, biblical, canonized, catechism, Deuteronomy, etc., etc

I have made such counts for fifty-four of the persons, for twenty-one of whom certain criterion scores are available, using the rubrics listed below

- 2. Interest in things and mechanisms
- 3. Interest in persons and feelings and acts
- 4. Interest in animals
- 5. Interest in words
- 13. Interest in art
- 14. Interest in music
- 15. Interest in beauty
- 24. Interest in neatness
- 31. Interest in church and religion
- 54. Interest in food
- 64. Interest in clothes and personal adornment
- 61. Tendency to think of the bright side, pleasant facts, etc.
- 62. Tendency to think of the dark side, unpleasant facts, etc.
- 100. Self-indulgence
- 111. Puritanism

No word was ever counted for more than one rubric. Words of the Thorndike 10,000 list of the most used words in books, newspapers, etc., were scored by a uniform key. Words outside it were scored (for 25 of the 54 persons) by one person, preserving approximate uniformity.

THE RELIABILITIES OF THE SCORES

Words from A through K were used to provide one random half-score, and words from L through Z to provide another ¹. It would have been well to use also scores made from the writings on alternate days. But the labor of such double entering seemed prohibitive. Scores of two sorts were

¹ The dividing point was put earlier or later if the above method gave a very uneven division

recorded: (1) the gross number of words, and (2) the percent which this was of the sum of the person's counts in all rubrics.

As I have shown elsewhere, the words written by some persons on some occasions are largely determined by the person's intent to have ideas and write words all related to the starting stimulus word. There is also a wide-spread tendency, as the experiment progresses, to change from thinking in strings of names of things, persons, qualities, acts, events, etc to thinking in sentences. This dilutes the 4000 words by many relational or colorless words (such as *a*, *and*, *as*, *be*, *if*, *in*, *of*, *it*, *the*, *when*, *who*). Persons vary greatly in the strength of this tendency, and also in the strength of the tendency to insert quotations. The second sort of score mentioned above frees the records from the influence of these last-named tendencies, and is the better one to use. It does, however, have the demerit of eliminating the influence of genuine differences in total average score in *all* rubrics.

Using these percentage scores, the correlations of half-score with half-score range from 0.2 to 0.7, indicating reliabilities of from 0.3 to 0.8 from the use of all the 4,000 words written that were inside the Thorndike 10,000.¹ These results are very disappointing. The reliabilities could be improved somewhat by multiple scoring, as by counting the response of *piano* under 2 (things) as well as under 14 (music), or counting *cathedral* under 15 (beauty) as well as 31 (church and religion). But this enrichment of the material will not avail much. We have with single scoring a median of 826 (range from 460 to 1,157) words per person written that are inside the Thorndike 10,000 and are in one or another of our scoring keys. Multiple scoring might raise the 826 to 950 or even 1,000, but the reliabilities would still be low.

The effect of the inclusion of the words a person writes which are outside the Thorndike 10,000 commonest words will be considered after the facts concerning the validity of the

¹ The reliability coefficients are as follows: things, 0.7; people, 0.6; animals, 0.3; words, 0.5; art, 0.7; music, 0.7; beauty, 0.5; neatness, 0.6; church and religion, 0.5; food, 0.8; clothes and adornment, 0.7; pleasant rather than unpleasant ideas (61/62), 0.8; self-indulgence, 0.7; Puritanism, 0.3.

scores for words within the 10,000 (i.e. their significance as indicators of the person's real interests) have been presented

THE VALIDITY OF THE SCORES

I have used two checks on validity. The first is the correlations with the scores for interests obtained from the extensive questioning reported in the *Journal of Applied Psychology* in June, 1936 (Vol 20, pp 285-313).² By this check, the free-association scores are disappointing, the correlations average very low (near 0.10). The blame doubtless lies in part with the scores obtained from questioning, which have only a dubious validity, but the lack of agreement is disappointing.

² As samples of the questions, we may quote those relating to "things," "people," and "music." They were as follows

Things

Manual training
Shop-work
Trade work of any sort
Cooking
Domestic science (in general)
Repairing an automobile
Working with tools
Sharpen a knife
Take a clock apart and put it together
Do picture puzzles
Do mechanical puzzles
Be a cabinet maker
Be an electrician
Be an inventor
Be a plumber
Be a repairer of typewriters
Spend an afternoon visiting a shoe factory
Make ship models
Clean a bicycle
Oil a sewing machine

People

Bargaining
Selling to a customer
Going on errands
Go around applying for a job
Working as a guide on a sightseeing trip
Be a book agent
Be a life insurance agent

Be an ambassador or diplomat
Be a chief clerk in an office
Be a conductor on a railroad
Be a politician
Be a secretary to a senator
Be a social secretary to a society lady
Read the personal column in a newspaper
Spend an afternoon making social calls
Take pictures of insane people

Music

Music
Singing
Playing piano, violin or other instrument
Going to concerts
Listening to music
Go to a good concert
Spend an afternoon listening to Chinese music with explanations
Go to an organ recital
Go to a concert by a college glee club
Listening to bird songs
Take a trip to Mexico to collect phonographic records of Indian music
Learn that if you can study for three years you can have a great career as a singer
Try to learn to play the flute

The second check is the correlations with ratings for the traits in question by two men who had been working with the persons for some months¹ I use interest in animals, interest in art, interest in music, interest in words, and interest in the church and religion The correlations are very low, from 0 to 0.3. Here also part of the blame doubtless lies with the ratings of the two men, but only a part.

The plain fact is that when we take, from 4,000 words written by a person in 100 sets of 40 each spread over a month, those included in the commonest 10,000 words, and score them reasonably as indicators of interests, the scores show very little correspondence with either the scores obtained from questions such as are used in tests of interests, or those obtained by ratings made by acquaintances Nor would increasing the associations and questions and raters a hundred-fold raise the amount of correspondence to more than 0.3 or 0.4² Such trains of thought written in formal tests are revealing, but they do not reveal much. The correlations with other measures of interests tend to be positive, but extremely low. Words written as serial associations reveal the nature of a person only in part and confused by irrelevant factors Some gluttons may not think much about foods when they are writing words, the actual presence of foods or hunger may be necessary to evoke their interest Love of music may not cause a person to think much of music when he is writing words or sentences, and similarly for other interests

Indeed our results cast some doubt upon the assumption that a person's natural, ordinary thinking reveals his interests perfectly. In so far as it is in the form of words, it, too, may be an imperfect index. It is not certain that "as a man thinketh in his heart, so is he," in the sense that so will he behave *in toto*. Some of our cravings and motives may be

¹ They correlate one with another about 0.8, but the two raters may well have been afflicted by similar errors

² The reliability coefficients from the questions were as follows. things, 0.9, people, 0.6; animals, 0.8, words, 0.8; art, 0.8, music, 0.8, beauty, 0.6, neatness, 0.9; church and religion, 0.7, food, no data, clothing, no data; indulgence, 0.5, Puritanism, 0.6

dumb, or at least inarticulate; conventionality and insincerity may direct our secret thoughts as well as our observed deportment.

Nothing of what has been said so far requires alteration if the words written by a person which are not in the commonest 10,000 are included in his score. Using the records from 25 persons, I have computed reliability coefficients and correlations with the question-test criterion (but this was available for only 10 of the 25). The number of words which were taken as indicative of one or another of the interests studied (and also the interest in books) ranged from 65 to 800 with a median of 188. Using the percentages obtained by dividing the score for each interest by the sum of all such scores, the reliability coefficients are higher than they were for the commoner words in spite of the smaller numbers of words. The validity measures are a little higher, but still very low. The correlations between the scores on the same interest by words inside and by words outside the 10,000 are approximately as high as their reliabilities permit, showing that the two scores measure the same functions.

The use of long serial associations is less promising as a result of our study than it seemed *a priori*. We are led to conclude that the nature of the words written in such tests will be useful in the practice of measuring interests, attitudes, and other personal traits only as one feature of a team of tests, not as a sole reliance, and that the yield for a given expenditure of time in testing and scoring will be smaller than naive deductions from the psychology of trains of thought would predict. Such tests do have the great merit of being relatively free from certain limitations and dangers which attach to a person's rating of his likings for music, art, etc., and to his answers to detailed questions of the sort found in the instruments devised by Strong, Thurstone, Woodworth and others. But the scores give small returns for much labor.

‡

Free associations in the form of single responses or very short series may differ in important ways from those in the

series of forty each studied by us. Moreover, we have used words occurring anywhere in the person's thinking, not words as evoked by specific words.¹ It would not therefore be right to take our results as a condemnation of the ordinary verbal association test as a diagnostic instrument. It does have the merit that a record, easily and quickly obtainable, and usable in a fairly effective form with groups as a pencil and paper test, can be put to many uses. Certain associations do testify to intelligence, others to abnormality, others may indicate "conflicts," or at least give clues useful in locating "conflicts"), others may give evidence of the strength of interests. The one stone may injure many birds. I fear, however, that it rarely kills any of them. And the cost in time and need of special ability in scoring such a test are serious defects. Psychologists should continue to explore the possibilities of 200 or 400-word association tests as *candidates* for inclusion in a general inventory and appraisal of a person. But it will be prudent not to expect as much from them as we have in the past.

¹ It would be possible to investigate the significance of the associations evoked by specified words in these serial-association records. If, for example, the word *orchestra* occurs five times in A's record and also in B's and is followed in A's record by *beautiful, conductor, out of tune, Beethoven* and *Brahms*, and in B's by *tedious, pay, dance, school* and *club*, we should expect A to have a stronger musical interest than B. The arrangement of scoring keys and of systems of computing scores for the general use of this method, would be very difficult, and their operation would be well-nigh impracticable. This type of scoring should probably be restricted to single associations, as in the work of Rosanoff and Kelley. Consequently, I have not explored its possibilities or determined its values in the case of the 4000-word records.

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SOME BIOCHEMICAL INVESTIGATIONS ON THE CRYSTALLINE TOBACCO-MOSAIC VIRUS PROTEINS *

W. M. STANLEY

(Read January 2, 1937)

THE discovery by Iwanowski (1) in 1892 that the juice from tobacco plants infected with a mosaic disease remained infectious after being passed through a filter which removed all ordinary living organisms is generally regarded today as being the first demonstration of the group of infectious agents that we now call viruses. In 1898 Loeffler and Frosch (2) announced the discovery of the first animal virus, that of the foot-and-mouth disease. The same year Beijerinck (3) confirmed Iwanowski's filtration experiments, but chose to regard the entity responsible for the mosaic disease, not as being bacterial in nature as had Iwanowski, but as a new type of infectious agent. Since that time many diseases of plants, animals and man have been found to be caused by viruses. The exact nature of viruses has, however, been a matter of some confusion, for they have been regarded variously as invisible forms of ordinary bacteria, as a new kind of invisible living organism, as protozoa, as unusual products of cellular metabolism, as enzymes, and as different kinds of inanimate chemical substances. Nevertheless, the basic properties of viruses, whether plant or animal, are strikingly similar and it seems likely therefore that the problem of the nature of viruses is a fundamental and common one. There should be, therefore, from the standpoint of this fundamental problem, considerable latitude in the selection of a virus as a subject for study. In the past, because of training and experience, human pathologists have usually selected viruses affecting

* Abstract of a paper presented before Section N of The American Association for the Advancement of Science in the hall of The American Philosophical Society in Philadelphia on January 2, 1937.

man, animal pathologists have usually selected animal viruses, and plant pathologists have usually selected plant viruses as subjects of study. A chemist entering this field would not be handicapped because of training or experience, and would be free to make a selection entirely on the basis of the desirability of the virus as a subject for study. It is obvious that a virus should possess certain properties in order to be an ideal subject for experimentation. It should be readily available so that an abundant supply of starting material would be assured. It should be stable so that it could be subjected to various treatments without loss of activity. It should be highly infectious, readily transmissible, and capable of being titrated with a reasonable degree of accuracy so that it could be handled and measured without difficulty. Of all the viruses, plant or animal, tobacco mosaic is outstanding in possessing the desirable properties just enumerated. It was, therefore, selected as the subject for a chemical investigation.

After much preliminary work, which need not be detailed here, it was found possible to isolate from mosaic-diseased Turkish tobacco plants a crystalline protein possessing the properties of tobacco-mosaic virus (4). Figure 1 is a reproduction of some crystals of tobacco-mosaic virus protein. This material contains 16.5 per cent nitrogen, about 50 per cent carbon, 7 per cent hydrogen, and 0.1 or 0.2 per cent ash, and is optically active having a specific rotation of -0.43° per mg. of nitrogen. The crystals of the material are small, averaging about 0.02 to 0.03 mm. in length, and give a regular crystalline pattern on X-ray analysis (5). The material gives the usual color reactions for a protein and does not give a test for carbohydrate. It is precipitated from solution by salts or by the usual protein-precipitating agents. The protein is isoelectric at pH 3.3 and is quite soluble at neutral or alkaline hydrogen ion concentrations, but becomes less soluble as its isoelectric point is approached and is insoluble at the isoelectric point. When solutions of the protein are made more alkaline than about pH 11 or more acid than about pH 1, or are heated to about 75° C., the protein is

denatured and the virus activity is lost. The protein is not digested by trypsin, but is slowly digested by pepsin with loss of virus activity.

Many tests have indicated that the crystalline protein is about 500 times more active than the starting material. The activity would be expected to lie in this range, for 0.2 per cent by weight, or about a part per 500, of the diseased plants was isolated in the form of crystalline protein. One cc. of a solution containing but 10^{-6} grams per cc. of the protein has usually proven infectious. The protein has been found to be homogeneous with respect to isoelectric point and molecular weight, and to have a molecular weight of about 17,000,000 (6, 7), a value considerably larger than that of any other known protein and which, on the basis of a spherical molecule, corresponds to a protein molecule having a diameter of about 35 millimicrons. Although the protein passes a Berkefeld W filter, it is held back by collodion filters through which proteins such as egg albumin readily pass. Filters which hold back the protein also hold back the virus activity, and it has not been found possible to separate the virus activity from the protein by means of filtration through collodion or other types of filters. The virus activity, chemical composition, isoelectric point, molecular weight, X-ray diffraction pattern and optical rotation of protein obtained from many different lots of starting material are the same. Furthermore, these properties remain constant on careful recrystallization of the protein 15 times, on fractional crystallization, or on fractionation by adsorption on and elution from celite.

The sera of animals injected with a solution of the crystalline protein give a precipitin test when mixed with infectious juice or with solutions containing but 10^{-6} grams per cc. of the crystals, and fail to give a precipitate when mixed with the juice from normal plants. Antiserum to crystalline protein has a neutralizing effect *in vitro* on virus activity not possessed by normal serum. Treatment of the active protein with hydrogen peroxide, formaldehyde, nitrous acid, or ultraviolet light produces inactive native proteins that, although

slightly altered chemically, retain certain chemical and serological properties characteristic of the virus protein (8). Under the microscope the crystals of inactive proteins are indistinguishable from those of active protein. The sera of animals injected with a solution of inactive protein give a precipitate when mixed with solutions containing but 10^{-4} grams per cc. of either active, or inactive protein and the sera of animals injected with virus preparations give a precipitate when mixed with a solution containing as little as 10^{-4} grams per cc. of inactive protein. The sera of animals injected with a solution of inactive protein have a neutralizing effect *in vitro* on virus activity not possessed by normal sera. This point may prove to be of importance, for it is a demonstration that a virus can be inactivated under certain conditions without seriously changing its immunological properties. Some of our earlier preparations of crystalline protein were subjected to a serological study by Chester (9). Perhaps of greatest interest was the finding that by the Schultz-Dale technique the virus protein gave no anaphylactic reaction. It is possible that the high molecular weight of the virus protein may be responsible for this result.

The unusual, high molecular weight protein has not been found to exist in normal plants, hence it seems likely that the protein is peculiar to mosaic-diseased plants. Since many different species of plants are susceptible to the mosaic disease, it seemed of interest to determine whether or not other susceptible plants, including those distantly related to tobacco, would also contain this peculiar protein following infection with the mosaic virus. It was found possible to isolate this same protein from mosaic-diseased tomato plants (10) and either the same or a very closely related high molecular weight crystallizable protein from mosaic-diseased spinach and phlox plants. The isolation of the protein from diseased phlox plants is of especial interest and significance, since this plant is so far removed from tobacco that there is no serological relationship between the protein from normal tobacco plants and that from normal phlox plants. Thus, two dif-

ferent plants, the normal constituents of which are serologically unrelated, are able, following infection with the mosaic virus, to build up or synthesize proteins that appear to be chemically and serologically identical. There is evidence that in the plant tobacco-mosaic virus may in some way become changed or mutate and give rise to new strains (11, 12, 13). It seemed of interest to study the protein content of plants diseased with such strains of virus and to determine whether the mutation of virus is accompanied by any change in the protein which is produced. As a result of this study, three high molecular weight crystalline proteins have been isolated from Turkish tobacco plants infected with a masked, a yellow, and a single-lesion strain of tobacco-mosaic virus, respectively (14, 15). These three proteins, although apparently related to each other and to the crystalline protein from plants infected with ordinary tobacco mosaic, have been found to possess physical and chemical properties that distinguish them from each other and from the tobacco-mosaic virus protein. Thus, four different strains of tobacco-mosaic virus have been found to give rise to four different crystallizable, high molecular weight proteins. The results indicate that, when tobacco-mosaic virus mutates and gives rise to a new strain, this change is accompanied by the production of a new protein.

The fact that the crystalline protein from many different batches of starting material has the same chemical composition, isoelectric point, optical rotation, and biological activity, and that these properties remain constant during many recrystallizations and following drastic fractional crystallization, the fact that it was found impossible to separate the activity from the protein by means of filtration through colloidion or other types of filters, or by centrifugation of the protein from solution under a variety of conditions (16), the fact that the absorption spectrum of the protein agrees essentially with the destruction spectrum of the virus activity (17, 18), the homogeneity of the protein with respect to size and isoelectric point, the isolation of the protein from plants

distantly related to tobacco, the isolation of different proteins from plants diseased with different strains of tobacco-mosaic virus, and the fact that any change in the protein is accompanied by a change in virus activity are all indications that the virus activity is a property of the protein. In view of the complete absence of any contradictory evidence, it is felt that the results fully justify the conclusion, for the present at least, that this unusual, high molecular weight protein is actually tobacco-mosaic virus.

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PLATE I

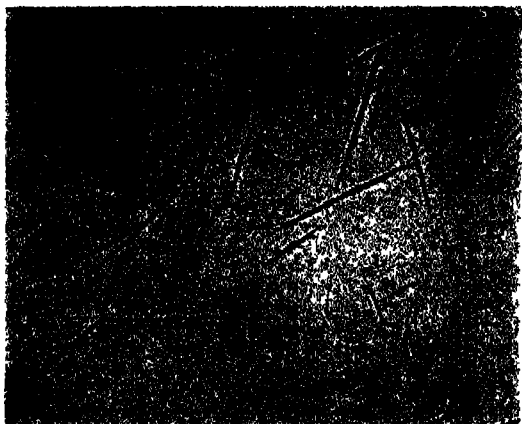


FIG 1 Crystalline tobacco-mosaic virus protein $\times 675$ (Photograph
by J A Carlile)

THE ULTRACENTRIFUGAL STUDY OF VIRUS PROTEINS

RALPH W. G. WYCKOFF

(Read January 2, 1937)

OVER the last year and a half we have been developing at The Rockefeller Institute a simple air-driven ultracentrifuge¹ which is proving to be a fruitful tool in the study of virus proteins. With this ultracentrifuge analyses² made of a series of tobacco-mosaic virus proteins³ have been surprisingly helpful guides to further research. The same experiments indicate that by ultracentrifugal procedures alone pure virus protein can be prepared direct from the juice of infected plants.

Ultracentrifugal analysis was originated by Svedberg⁴ about 12 years ago; since then it has been steadily improved through his efforts and those of his students. The fields needed for molecular sedimentation are very great—tens to hundreds of thousands times gravity—and the technical difficulties connected with this kind of research are considerable. The apparatus of Svedberg has been so expensive to build and to operate that only within the last year have duplicates been made.

This costliness of existing equipment has led to a number of efforts⁵ to simplify the necessary mechanical equipment. The most important feature in any such simplification is obviously the choice of a motive power less elaborate than Svedberg's oil turbine. Beams' development⁶ of a stable

¹ F. Biscoe, E. G. Pickels and R. W. G. Wyckoff. *Jour. Exp. Med.*, 64, 39. 1936.

² R. W. G. Wyckoff, J. Biscoe and W. M. Stanley. *Jour. Biol. Chem.*, 127, 57. 1937.

³ W. M. Stanley. *Science*, 81, 644. 1935; *Jour. Biol. Chem.*, 125, 673. 1936.

⁴ For bibliography see T. Svedberg. *Nature*, 22, 225. 1934.

⁵ See for example J. W. McBain and C. M. O'Sullivan, *Jour. Amer. Chem. Soc.*, 57, 2611. 1935.

⁶ J. W. Beams and E. G. Pickels. *Rev. Sci. Instr.*, 6, 299. 1935; etc.

air turbine with pendant rotors has provided a very satisfactory solution to this problem

Our ultracentrifuge was accordingly built around the air turbine and employs rotors of the same large size as Svedberg's. It thus is capable of yielding results of the same degree of accuracy. The air turbine itself is simple and inexpensive to build and will operate on the supply of compressed air available in most research laboratories. The cost of our centrifuge has been still further decreased by making rotors of duralumin and other light metal alloys instead of steel¹ Duralumin is a material which has a specific tensile strength comparable with that of steel, fortunately it is easily machined when in its condition of maximum strength. All rotors no matter what the material from which they are made will fail after running at high speeds for a longer or shorter time. Duralumin has the further advantage over steel that when this failure occurs the rotor is carrying less energy and will do much less damage. For this reason less protection need be built into an ultracentrifuge using light rotors, thus both the initial and maintenance costs are reduced and an apparatus is produced that is not so cumbersome to handle.

Nearly all the analytical observations to be made on virus proteins will involve measurements of rates of sedimentation. Our air-ultracentrifuge arranged for such studies is shown in Fig. 1. Tobacco-mosaic virus proteins are the only disease-producing agents upon which such ultracentrifugal analytical results have yet been published. They have been studied both by Svedberg² and ourselves.³ Svedberg was primarily interested in estimating molecular size, we were concerned in investigating different virus strains. Svedberg found that the virus protein sedimented more rapidly, and hence was heavier, than any other known substance in true solution; his estimate of the molecular weight is around 17,000,000. In confirming this high sedimentation rate we found that it was different for different strains—the aucuba coming down

¹ J. Biscoe, E. G. Pickels and R. W. G. Wyckoff. *Rev. Sci. Instr.*, **7**, 246. 1936

² I. Eriksson-Quensel and T. Svedberg. *Jour. Amer. Chem. Soc.*, **53**, 1863. 1936

³ R. W. G. Wyckoff, J. Biscoe and W. M. Stanley. *Op. cit.*

much faster than the ordinary strain. We also found that more than one species of heavy protein was often present in infectious juice and that the ratio of these species varied with the age of the plant as well as with the initial infecting agent; thus it became apparent that the tobacco-mosaic virus proteins consist of a family of related but physically distinguishable compounds. Our measurements likewise demonstrated that host plants as unlike as tobacco, tomato and phlox all build virus proteins that are identical, at least in physical properties. Analytical runs such as these have given other useful information about tobacco-mosaic virus preparations. For example, the degree of sharpness of sedimenting boundary is an index of the amount of molecular heterogeneity brought about by chemical treatments (including those of concentration) to which the virus has been subjected. Ultracentrifugal analysis also provides a useful way of estimating the purity of a concentrated virus protein sample. Normal plant proteins (and equally the proteins extracted from normal animal cells devoid of special function) have small molecules not larger than those of egg albumen. Because they are not sedimented by the fields needed to bring down virus proteins the ratios of the absorption of light above and below the virus boundary and through an equivalent column of air are measures of the purity and the concentration of the preparation.

The analytical observations just described, which were made with our ultracentrifuge, could equally well have been carried out on the classical machine of Svedberg. But as so often happens when a new kind of apparatus is made, the air ultracentrifuge quickly proved to have potentialities¹ in addition to those of the machine which inspired it. The most striking mechanical difference between Svedberg's ultracentrifuge and ours, aside from their different motive powers, lies in the fact that whereas his turns about a horizontal axis, ours rotates about a vertical axis. This simple shift of axis makes it possible to centrifuge larger volumes of liquid, and

¹ J. H. Bauer and E. G. Pickels *Jour. Exp. Med.*, **64**, 503, 1936, R. W. G. Wyckoff. *Science*, **84**, 291. 1936, R. W. G. Wyckoff and R. B. Corey *Science*, **84**, 513, 1936

to collect easily without their remixing, the fractions that result. In the analytical runs to which ultracentrifuging has hitherto been restricted, the cell contains only a few drops of solution and this ordinarily cannot be recovered in separate layers at the end of the experiment. We are now routinely ultracentrifuging more than 100 cc. at a time under circumstances that give no heating of the liquid even after a full day's running. The fields used in our work thus far range up to 60,000 to 70,000 times gravity. But there is every reason to believe that our rotors could be run at higher speeds; and when the need arises greater volumes can be handled. This phase of the work has not been going on for a long enough time so that its practical limitations are known, nor can the most efficient design of apparatus be specified. We are, however, making studies of rotors of several shapes, capacities and materials to give this information.

An air-ultracentrifuge arranged for quantity centrifuging is shown in Fig. 2. The driving mechanism, which is the one now employed on all our ultracentrifuges, is an improvement¹ over the simple turbine of the earlier apparatus. It has backwardly-directed jets and flutings for quick and safe stopping and a set of compression screws to give easy adjustment of level. The assembled turbine and quantity rotor removed from the protecting steel pot can be seen in Fig. 3. The particular design of rotor will, of course, depend on the kind of problem for which it is used. One has been described for the concentration of yellow fever virus.² Ours³ operates on the principle of the familiar angle centrifuge. A block of metal of suitable size, capped with a cover made vacuum-tight by a rubber gasket (since the whole must turn in a vacuum) is drilled to accommodate containers for the liquid to be centrifuged. Two sizes, one holding 7 cc., and the other 17 cc., are employed (Fig. 4).

The preparation of pure viruses in large amounts, which must be one of the immediate goals of research upon them,

¹ R. W. G. Wyckoff and J. B. Lagedin. *Rev. Sci. Instr.*, March 1937.

² J. H. Bauer and E. G. Pickels. *Op. cit.*

³ R. W. G. Wyckoff and J. B. Lagedin. *Op. cit.*

involves two problems. One is the concentration of virus without loss of biological activity, the other involves freeing the virus from the large mass of organic impurities (normal proteins, cell debris and the like) that ordinarily contaminate it. Tobacco-mosaic virus protein has been repeatedly concentrated, purified and crystallized from the juice of infected plants merely by centrifugation. When the juice of such plants is clarified by low speed centrifugation and then ultracentrifuged, about 90 per cent of the protein and practically all the virus activity¹ is found concentrated in a solid pellet at the bottom of the tube. As runs in the analytical ultracentrifuge demonstrate, protein in the supernatant is of low molecular weight and nearly all in the pellet has the large sedimentation constant characteristic of the chemically prepared virus protein. Besides this virus protein, which is already crystalline,² there will be present a considerable quantity of chlorophyll and brown pigment. Purified virus protein can be obtained by extracting the dark-colored pellet so that the protein goes into solution leaving the pigment in a coarsely flocculent form readily removed by low speed centrifugation. A second ultracentrifugation will then throw the virus protein down in a cleaner crystalline form. Such a process of successive ultracentrifugal crystallizations, interspersed with low speed centrifugings to remove flocculated impurities, can be repeated as often as desired without appreciable loss of virus activity. This purely physical mode of preparation is of value in ascertaining whether chemically prepared virus protein has been altered during its isolation. Its primary importance, however, lies in supplying a way of isolating quantities of virus proteins which cannot be chemically concentrated and purified either because they are too unstable or are present in only very small amounts.³

In using the quantity ultracentrifuge it is important to know how effective it is in sedimenting the large virus par-

¹ W. M. Stanley *Jour. Biol. Chem.*, **117**, 755 (1937).

² R. W. G. Wyckoff, and R. B. Corey *Op. cit.*

³ Examples of such use will be given in a forthcoming paper by W. M. Stanley and R. W. G. Wyckoff, *Science*, **86**, 181 (1937).

ticles and separating them from small molecules that may be present. This effectiveness will, of course, vary with the virus material and depend on such factors as the intensity of the centrifugal field and its duration, the viscosity of the medium and the length of the sedimenting column (which in turn is determined by the design of the rotor). With tobacco-mosaic virus, results of the following character are obtained.¹ After centrifuging infectious juice for three hours in a maximum field of 40,000 times gravity, less than one part in a hundred thousand (10^{-6}) of the original activity was left in the supernatant; with a fairly strong and viscous solution (10 mg per cc.) of the purified virus protein the upper half of the supernatant retained between 10^{-4} and 10^{-5} of its activity. Egg albumen, which is comparable in size with the heavier components in normal plant juice, not only gave no solid precipitate from a 1.5 per cent solution run under similar conditions but showed only a slight concentration of its bottom-most layer (to 1.6 per cent protein).

The illustrations that have been given of the application of analytical and quantity ultracentrifugation of tobacco-mosaic virus have been drawn from our published work. Such analytical tests and the procedures outlined for concentration and purification can, however, be applied to other virus materials. When we seek to transfer our experience with tobacco-mosaic virus proteins to the causative agents of other virus diseases there arises first the question of whether the centrifugal fields at our disposal are adequate to concentrate and sediment all known viruses. This can definitely be answered in the affirmative. Available data on plant viruses suggest that they do not depart widely from one another in size. Animal viruses range downwards in a more or less unbroken series from the limit of visibility (0.2–0.1 μ) to about 10 μ in diameter. It is easy to calculate (from crystal structure determinations on simple organic crystals, for example) the approximate size of a spherical protein molecule of given weight. Tobacco-mosaic virus protein with a weight

¹ W M Stanley. *Op cit*

of ca. 17,000,000 should have a molecular diameter of ca. $35\ \mu\mu$. Thus it lies midway amongst the animal viruses. Those viruses which are supposed to be larger than $35\ \mu\mu$ ought to sediment as easily as does the tobacco-mosaic virus and such has indeed proved to be the case with one we have tried. There is evidence that the smaller ones too fall well within the present range of experiment. The activity of the small yellow fever virus has been concentrated;¹ with fields far below the maximum now available to us, we have thrown down in solid form hemocyanin (diameter = ca $16\ \mu\mu$), horse pneumococcic antibody (diameter = ca. $11\ \mu\mu$) as well as the staphylococcus bacteriophage² which is supposed to range with the smallest viruses.

The technical problem of concentrating virus activity by ultracentrifugation may, therefore, be considered as solved. Ultracentrifugal procedures will effect the equally essential purification of tobacco-mosaic virus, it is natural that they should work equally well on other plant viruses. The degree of success they will have, either alone or in conjunction with suitable chemical treatments, in providing a supply of pure animal viruses can only be told after much further work.³

SUMMARY

An air ultracentrifuge has been developed which is giving two-fold help in the study of viruses.

(1) Analytical runs with it, besides furnishing a measure of the size of the virus molecules, can tell whether a preparation is pure and what may be the molecular weight of its impurities, whether a virus consists of one molecular species or a family of related proteins, etc

(2) Runs in which large volumes are ultracentrifuged in fields sufficiently great to sediment any of the known viruses

¹ J. H. Bauer and E. G. Pickels. *Op. cit*

² J. H. Northrop. *Science*, **84**, 90. 1936

³ See in this connection the recent isolation by the ultracentrifuge of a homogeneous protein carrying virus activity from infectious rabbit papillomas, J. W. Beard and R. W. G. Wyckoff, *Science*, **88**, 201 (1937).

provide the basis for a method of preparing pure virus protein without having recourse to chemical treatment. This method opens up the way to the study of viruses which, unlike that of the tobacco-mosaic disease, are relatively unstable or present in only small amounts

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PLATE I

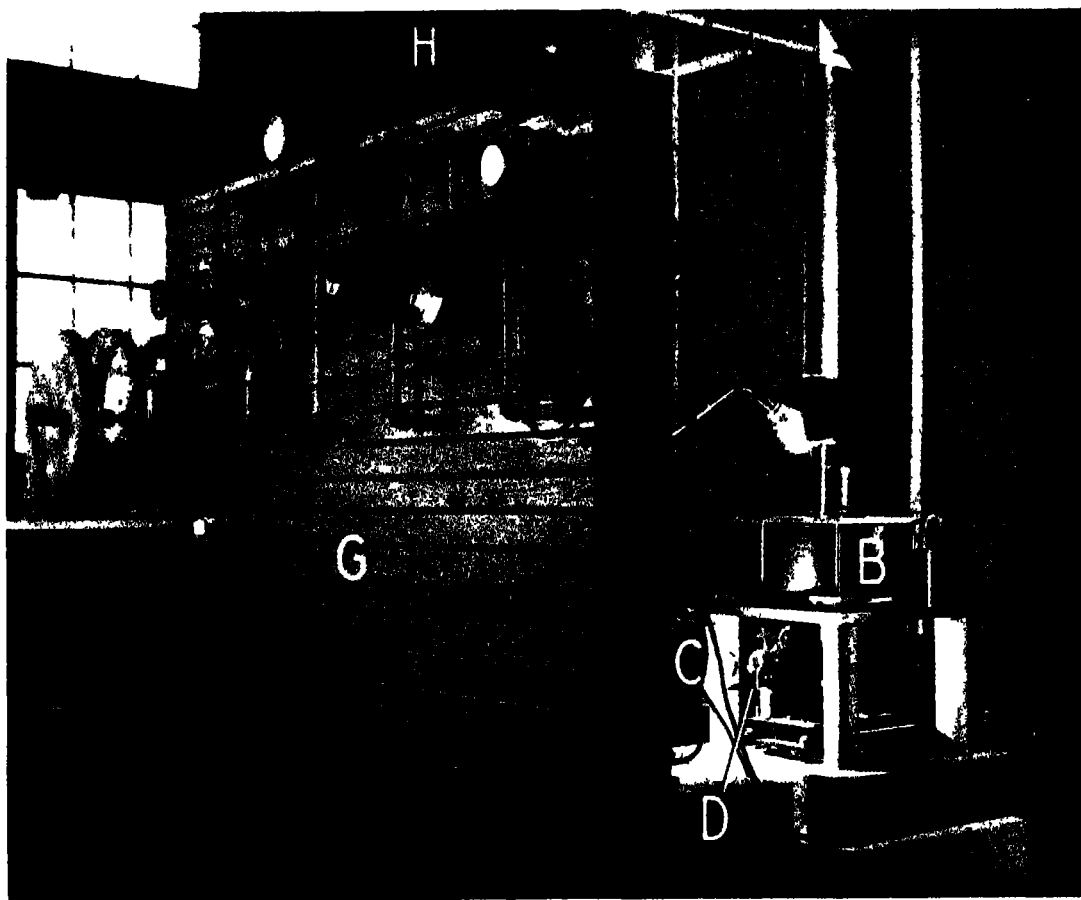


FIG. 1. An air-ultracentrifuge arranged for measurements of rates of sedimentation by the absorption method. The driver (*A*) is connected with the rotor in the steel pot (*B*) by a thin steel shaft. The solution to be analyzed is contained in a cell capped with quartz windows and set near the periphery of the rotor. Sedimentation of protein molecules in this solution can be followed by an optical system consisting of a quartz mercury lamp (*C*), filters and mirrors (*D* and *E*) and photographic lens (*F*). The camera (not shown in the picture) is at the end of the tube containing *F*. Air-pressure valves and gauges for driving, controlling and stopping the ultracentrifuge are shown mounted on the sand-filled barricade (*G*). Speed is determined by the stroboscope (*H*).

PLATE II

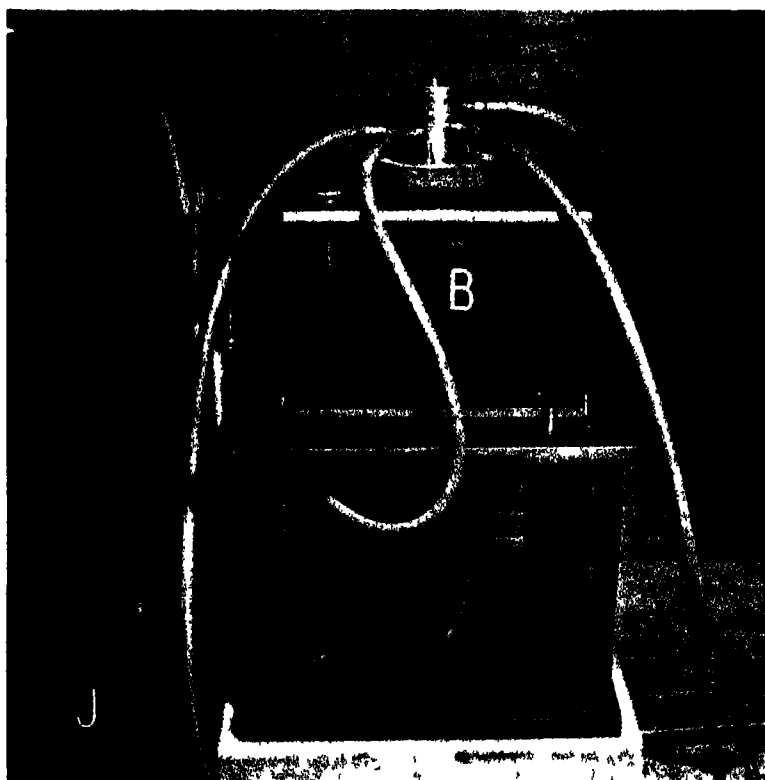


FIG. 2. An ultracentrifuge arranged for quantity centrifugation. The rotor holding the solutions (Figs. 3 and 4) is contained in the steel pot (B) and driven by the mechanism (I). The pump for evacuating (B) is shown at (J).

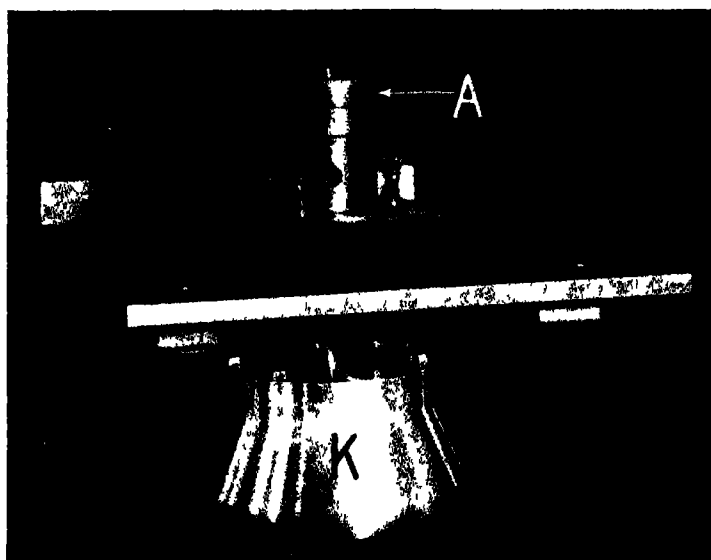


FIG. 3. The quantity ultracentrifuge of Fig. 2 removed from the vacuum pot to show its suspended rotor (K).

PLATE III



FIG. 4 A quantity rotor with its cover removed to show the six holes for 17 cc tubes

LABILE BACTERIAL ANTIGENS AND METHODS FOR THEIR PREPARATION AND PRESERVATION *

STUART MUDD

WITH E. I. CZARNETZKY, HORACE PETTIT AND DAVID LACKMAN.

(Read January 2, 1937)

PROGRESS in any branch of chemistry is necessarily limited until single reagents become available. In particular, investigation of the chemical and serological mechanisms underlying infectious disease has been limited by lack of pure reagents in the form of single, native antigens and antibodies. Practical procedures such as active and passive immunization and serum therapy have suffered similar limitations from the fact that the immunizing agents used have been complex, frequently toxic and have often undergone serious alteration in the course of preparation.

Discoveries of the past few years have particularly served to emphasize the lability of a number of essential immunizing antigens, the V_i antigen of the typhoid bacillus,¹ the capsular polysaccharide of the pneumococcus,² the labile agglutinogen of vaccinia bodies,³ and the labile antigens of hemolytic streptococci,⁴ serve as examples of antigens the activity of which could not withstand the classical methods of chemical extraction and purification.

The capsular polysaccharides of pneumococcus Types I, II and III have recently been separated in closer approximation to

* This work has been aided by grants from the United States Public Health Service and from the Abington Memorial Hospital.

¹ Felix, A., and Pitt, R. M., *Lancet*, 1934, 2, 186.

² Heidelberger, M., Kendall, F. E., and Scherp, H. W., *J. Exper. Med.*, 1936, 64, 559.

³ Craigie, J., and Wishart, F. C., *Brit. J. Exp. Path.*, 1934, 15, 390.

⁴ Mudd, S., Pettit, H., Lackman, D., and Czarnetzky, E. J., *Proc. Am. Ass'n. Path. and Bact.*, *Am. J. Path.*, 1936, 12, 746. *Proc. Soc. Am. Bact.*, *J. Bact.*, 1937, 33, 63.

their native state,² utilizing the chloroform method of Sevag.⁵ The V₁ typhoid antigen has been obtained in this laboratory⁶ in cell-free, immunizing form after disintegration of virulent typhoid bacilli by intense sonic vibration of audible frequency in the laboratories of the Johnson Foundation for Medical Physics of the University of Pennsylvania.⁷ The labile surface antigen of *Streptococcus hemolyticus* (Lancefield Group A) has been isolated in antigenic form following disintegration of the streptococci by each of three physical methods.

1 The bacteria, in a dense suspension, are disintegrated by intense sonic vibrations of audible frequency.⁷ This method is satisfactory if equipment is available.

2 The streptococci are dried in vacuo from the frozen state,⁸ are transferred to a mortar, and liquid air is poured on them. They are ground with a pestle as the liquid air evaporates.⁹ This method is effective, but we have discontinued its use because of the danger of explosion of the liquid oxygen in the presence of organic matter, and because of the tendency of the gases evolved to scatter viable bacteria.

3 The streptococci are grown in mass culture, centrifugalized at high speed, and then transferred in the form of a heavy suspension directly to a special ball-mill. The mill with the bacteria in it is attached to a high vacuum line with a condenser interposed, and the bacteria are dried from the frozen state by the lyophile process.⁸ When the bacteria are dry, the mill is attached to a motor, and is operated in a bath of Dry-Ice in Methyl Cellosolve.¹⁰

After disintegration by any of these three methods the bacterial residue is taken up in saline solution, centrifugalized, and the supernatant fluid passed through a bacterial filter. Isolation of the labile surface antigen from the filtrate is accomplished by bringing the solution to a certain pH on the

⁵ Sevag, M. G., *Biochem. Z.*, 1934, 273, 419

⁶ Mudd, S., and Greaves, R. E., to be published

⁷ Chambers, L. A., and Floedorf, E. W., *Proc. Soc. Exp. Biol. and Med.*, 1936, 34, 631

⁸ Floedorf, E. W., and Mudd, S., *J. Immunology*, 1935, 29, 389

⁹ Czarnetzky, E. J., *Science*, 1936, 84, 355

¹⁰ Mudd, S., Shaw, C. E., Czarnetzky, E. J., and Floedorf, E. W., to be published.

acid side of neutrality. The antigen flocculates, and may be sedimented in the centrifuge. The sediment is soluble in 0.85 per cent NaCl solution. The antigen may be purified by solution in 70 per cent ethyl alcohol, with subsequent removal of the alcohol by distillation under high vacuum at 10° C.

Absorption of immune rabbit serum with the homologous labile antigens so prepared completely removes the type-specific antibodies which cause agglutination, promote phagocytosis and confer on mice passive protection against streptococci of the corresponding type. Injected into rabbits these labile antigens elicit antibodies.

These antigens if kept for a few days in the refrigerator or heated for one hour at 56° C. lose completely their power of combining with homologous antibody. This inactivation has been shown to be an oxidation reaction which is readily reversible. Thus when stored or heated in the presence of such reducing agents as cysteine or thioglycolic acid the antigen retains its activity; if inactivated by mild oxidation, the ability to combine with antibody may be restored by reduction with cysteine or thioglycolic acid.

When reduced by sodium bisulphite the labile antigen becomes lytic for red blood cells. Indeed it appears probable that the oxygen-labile streptolysin studied in culture filtrates by Neill and Mallory¹¹ and by Todd¹² is a derivative of the labile antigen.

Classification of the β -hemolytic streptococci into serological groups, which correspond broadly to grouping on the basis of pathogenicity and of biochemical reactions, has been accomplished by Lancefield.¹³ This classification depends upon the presence in each group of a characteristic carbohydrate detectable by the precipitin reaction. Subdivision of the group pathogenic for man (Group A) into serological types was also first accomplished by Lancefield on the basis of a type-specific protein-like substance "M." The M substances as prepared by Lancefield give type-specific precipitin

¹¹ Neill, J. M. and Mallory, T. B., *J. Exper. Med.*, 1926, 44, 341.

¹² Todd, E. W., *J. Path. and Bact.*, 1934, 39, 299.

¹³ Lancefield, R. C., *J. Exp. Med.*, 1933, 57, 571.

reactions with homologous antisera, but are not themselves antigenic

A comprehensive classification of Group A hemolytic streptococci into serological types has been achieved by Griffith¹⁴ on the basis of agglutination by type-specific sera. The classifications into groups by Lancefield and into types by Griffith are rapidly becoming accepted as standard by workers in the field.

The labile surface antigen when a part of the bacterial surface, corresponds in distribution and specificity to Griffith's type-specific agglutinin. When subjected to the chemical procedure used by Lancefield in preparing her type-specific M substance, this labile antigen breaks down into two fractions. One of these fractions exhibits the specificity and other properties of the M substance; the other fraction has the specificity of Lancefield's group carbohydrate. The labile surface antigen may be preserved by the lyophile process.

Another new fraction has also been isolated from β -hemolytic streptococci, although it is not necessary to disrupt the organisms to obtain it.¹⁵ It can be obtained in crude form by extraction of the lyophile processed organisms with moistened ethyl ether. This fraction can be further purified, and it has been shown that the pure product is homomolecular. A phosphorus-free derivative can be crystallized from water or alcohol as the sodium salt. Both the non-crystallizable material and the crystallizable material are able to hemolyze red blood cells up to a dilution of 1 in 40,000, and also act as leucocidins. The non-crystallizable fraction is stable to oxygen, heat and to acids and alkalis, and appears to be similar to the oxygen-stable hemolysin of Todd.¹⁵ It does not elicit antibodies when injected into rabbits in the pure form, but is precipitated by antisera prepared against any β -hemolytic streptococci, and can therefore be considered a haptin.

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¹⁴ Griffith, F., *J. Hygiene*, 1934, 34, 542

¹⁵ Czarnetzky, E. J., Morgan, Isabel M., and Mudd, Stuart, to be published.

FILTERABLE VIRUSES IN UPPER RESPIRATORY INFECTION

YALE KNEELAND, JR.

(Read January 2, 1937)

DURING the past ten years a considerable amount has been added to our knowledge of the genesis and mechanism of upper respiratory infection, and it is the purpose of this paper to review some of these investigations with particular reference to the work of Dochez and his collaborators. By the term "upper respiratory infection" I wish to indicate two diseases: one the so-called common cold—an acute communicable disease to which human beings are almost universally susceptible in greater or less degree—and the other, influenza—by which we mean an acute infection wherein the general or constitutional manifestations far overshadow the symptoms of local infection of the upper respiratory tract, although these latter are always present in at least sufficient degree to identify the nature of the disease. Now the common cold presents certain clinical variations in different climates and in different age-groups, and influenza may be sporadic, or epidemic, or pandemic, as it was in 1918. Nevertheless, in spite of these clinical variations the two diseases are sufficiently definite entities to be easily recognized.

The idea of a filterable virus as a causative agent in colds and influenza is by no means a new one. As long ago as 1914 Kruse in Germany published the results of experiments indicating the existence of a filterable virus in the common cold, but the lack of quarantine procedures in such experiments, and the failure of other investigators to confirm them, surrounded these early essays with an atmosphere of doubt, so that by 1920 the evidence against a filterable virus was very much greater than that in favor of it. The same situation, it may be added, existed in relation to influenza.

Our early work concerned itself simply with one question—*i.e.* was it possible to transmit an acute cold by means of bacteria-free filtrates of material derived from the upper respiratory tract of individuals with an acute cold. Numerous experiments of this type were made both in chimpanzees and human volunteers, under conditions of strict quarantine, and by the end of two years we had convinced ourselves that a filterable agent was indeed present that could initiate a typical common cold if introduced into the nasal passages of a susceptible human being or anthropoid ape. Attempts to show the presence of this agent in the secretions of normal individuals were entirely without success. It was concluded, therefore, that in all probability this agent was the causative one in colds, and that it belonged to the group designated as filterable viruses. From that point we went on to a study of its properties. In all the work to be described the presence of this virus has been tested by its ability to induce typical acute head colds in human volunteers under a technique of rigid isolation.

These first experiments were aimed to test whether the virus could be preserved for any length of time outside of the body. Our initial attempts at this were done with material under anærobic conditions—*i.e.* the original filtrate, usually concentrated by vacuum distillation, preserved under vaseline seal with cysteine—and by these means the virus was shown to remain fully active for at least a fortnight. We next attempted to discover whether serial passage of the virus through human volunteers would enhance its virulence. It was found easily possible to effect such a serial passage, but no enhancement of virulence could be demonstrated. Inasmuch as other filterable viruses can be cultivated in artificial medium provided that a small amount of living tissue is incorporated therein, it was considered of importance to determine whether cold virus would behave in a similar manner. Since we had previously shown that the virus could be preserved under anærobic conditions, the usual medium containing minced chick embryo tissue was modified by sealing and

incorporation of cysteine so as to maintain anærobiasis. Medium thus prepared was inoculated with a concentrated filtrate of the nasal secretions of an individual with an acute cold, incubated, and transfers made to fresh medium at intervals of a few days.

A large number of tests of different strains of virus so cultivated has been made, and in seven out of eight attempts we have been successful in initiating a culture of the cold virus—that is, the virus has been shown to multiply in artificial medium, for after a great number of transfers the material was still fully active in producing an acute experimental cold. That none of the original inoculum was still present was proved by the mathematical factor of dilution.

Experience has shown that cultures transferred at intervals of two to three days maintain their virulence better than if the transfers are made at longer intervals of time. Another observation of considerable interest is that after very prolonged cultivation in artificial medium there is a falling-off in virulence of the cultures, while we have obtained fully active material after eighty-odd transfers, the virulence of cultures that have been transferred more than one hundred times is very low indeed. Furthermore, we have not been successful in cultivating the virus under ærobic conditions, two attempts have been made in which ærobic cultures have been carried parallel to anærobic cultures of the same strain, the latter having repeatedly proven to be active. Neither of these attempts at ærobic cultivation was successful. Recently we have made one experiment in another method of cultivation. A number of investigators have used the chorio-allantoic membrane of the developing chick embryo as a medium for the propagation of filterable viruses, carried in this manner, the cold virus was found to be fully active in material derived from the third series of eggs through which it had been passed.

Further experiments in regard to the preservation of the virus have also been performed. It has been found that the original filtrate, if frozen at a very low temperature immediately after its isolation from the human source and desiccated

under a high vacuum, will retain its activity for at least four months. On the other hand, active virus in the tissue medium will not retain its activity even for a few days if treated by this method unless a small amount of gum acacia has been added beforehand.

This summarizes our knowledge of the virus of the common cold, in addition to these studies we have also made certain observations concerning the role played by the bacteria of the upper respiratory tract. In the first place, it is obvious that the suppurative complications of colds are due to bacteria, and in these cases it is believed that the bacteria act as secondary invaders. Their role in upper respiratory infections which do not present such suppurative manifestations is less easy to define. Certain pieces of evidence, however, have been collected in this regard. In the case of the anthropoid ape, cultures of the nares and nasopharynx made before and during an experimental cold quite regularly revealed a springing into prominence of certain pathogenic bacteria which were previously recoverable only with great difficulty. Furthermore, in a number of instances we observed a change in the type of *H. Influenzae* carried from the "R" to the "S," or type-specific form. At the end of the cold these organisms would revert to the "R" form, but in a subsequent experimental cold the shift would take place once more, and always to the same type-specific variety as was found before. Lastly, in an infant population it was found that colds were followed by a widespread dissemination throughout the colony of certain pathogenic bacteria, and that when the carrier rate of these bacteria became very high an outbreak of colds took on a more serious character, was attended by many febrile manifestations, and complications were frequent. From such observations it was possible to conclude that the cold virus favored the dissemination of pathogenic bacteria throughout the community, that it might "activate" them, so to speak, in the individual case, and might even alter their essential virulence. On the other hand, many bacteriological observations of experimental colds in adult volunteers have not

yielded any comparable findings. Our conclusion has been, therefore, that the cold virus probably can interact with bacteria in the ways indicated, but that the uncomplicated head cold in adults is a pure virus disease.

With this technique of investigation at our disposal it was natural that we should apply it to the problem of sporadic influenza. In summarizing our experiences with this disease it may be said that we have obtained material from influenza patients in four successive years, and of the four viruses studied three behaved in a manner very similar to the cold virus. In regard to the fourth strain a somewhat different result ensued. This was derived from a local outbreak of more than usual severity and cultivated anaerobically in tissue medium. Material from the eighteenth transfer of the culture was tested in three volunteers, one of these became ill with marked constitutional symptoms and an oral temperature of 101° . The other two suffered upper respiratory infections which were afebrile, but of these one had a rather marked constitutional reaction. Insofar as these few experiments can be interpreted, they merely indicate the presence of a virus in certain cases of sporadic influenza.

The discovery by Smith, Andrewes, and Laidlaw of a virus in epidemic influenza capable of infecting ferrets and the subsequent work of these investigators and of Francis in this country, has demonstrated that from certain severe epidemics of the disease strains of virus can be obtained which are similar to one another. In evaluating our results in the light of theirs it seems probable that there exist at least two types of virus—the cold virus, which can be cultivated anaerobically and will not infect ferrets, and the virus of epidemic influenza the properties of which they have so thoroughly described. In addition there is certain immunological evidence obtained by these workers in collaboration with Shope which suggests that the virus of the 1918 pandemic was another entity still.

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THE TRANSFORMATION OF THE VIRUS OF RABBIT FIBROMA (SHOPE) INTO THAT OF INFECTIOUS MYXOMATOSIS (SANARELLI)

GEORGE PACKER BERRY

(Read January 2, 1937)

IN A preliminary report a brief description was made of experiments which apparently showed that it had been possible to transform the virus of Rabbit Fibroma (Shope) into that of Infectious Myxomatosis (Sanarelli). Further studies, which support the original interpretation, are summarized in the present note.

In 1932 Shope discovered that the myxoma and fibroma viruses were immunologically related. We were able to confirm his observations and to extend them. Our findings were made possible by establishing myxomatosis in a new host, the cottontail (Genus, *Sylvilagus*) rabbit, in which host the infection did not kill. Thus, animals recovered from myxomatosis became available, a situation almost never realized with domestic (Genus, *Oryctolagus*) rabbits, for in this host the disease is almost uniformly fatal. We showed that infection with either myxoma or fibroma virus induced in domestic and cottontail rabbits a resistant state to both viruses and that this state was characterized in each variety of host by the development in the blood serum of neutralizing capacities for either virus. Thus, a basic relationship in the antigenic structure of the two viruses was indicated and led to the attempt to change one virus into the other by a method suggested by Griffith's studies in 1928 on the transformation of pneumococcal types.

In our first note we reported that transformation of fibroma virus into myxoma virus had occurred in each of eight experiments, employing two strains of fibroma virus

(Shope's original "A" strain, and one isolated by us in New York State from a wild cottontail and named the "Cayuga" strain) and a Brazilian strain of myxoma virus. In these experiments the virus of Infectious Myxomatosis was obtained from domestic rabbits which had been inoculated with a mixture of active fibroma virus and heat-inactivated myxoma virus. The rabbits received large amounts of the mixture by combined intracutaneous and intratesticular injection. The fibroma virus was a heavy suspension of pooled dermal and testicular fibromata; the myxoma virus to be heat-inactivated, a heavy suspension of primary skin lesions. The myxoma suspensions were inactivated in sealed glass ampoules for 30 minutes at temperatures of 60°-90° C. Transformation took place with 60°-75° C-material, but not with 90° C.-material. Suitable controls demonstrated that the heat-inactivated myxoma suspensions were alone unable to induce myxomatosis.

The ability of fibroma virus to change into myxoma virus under suitable experimental conditions appears to be a general characteristic, for we have successfully transformed each of the known strains of fibroma virus (in addition to those mentioned, Shope's "B," "C," "D," and "E" strains, kindly sent to us by Shope, and the so-called "mutant" strains, "IA" and "OA," kindly furnished by Andrewes). In each instance the myxoma virus obtained by "transformation" has been indistinguishable from ordinary myxoma virus. Transformation has been effected in the cottontail, albeit with more difficulty than in domestic rabbits. Furthermore, heat-inactivated myxoma suspensions derived from cutaneous and testicular lesions of cottontails (after 30-35 serial cottontail passages of myxomatosis) have served as "transforming agent" in both hosts. Considerable latitude in technique has been found to be compatible with transformation, thus it was not found to be essential that active fibroma virus and heat-inactivated myxoma virus be mixed *in vitro* before injection, for transformation took place when they were injected separately into different sites, either simultaneously or at different times.

Does heating at 65°-75° C. "completely" inactivate myxoma virus? This point is obviously crucial. Under no conditions, other than when active fibroma virus has been used, has it been possible to induce myxomatosis with heat-inactivated myxoma suspensions. We have studied 16 different lots of material in over 300 rabbits. When inoculated alone into normal rabbits, including serial passages, heated myxoma material has never given rise to significant lesions, and the inoculated animals have never been immunized. We have mixed heat-inactivated myxoma virus with a wide variety of substances, and inoculated rabbits prepared in a number of different ways, in order to provide, if possible, an "ideal locus" where any remaining active myxoma virus might manifest itself. Thus, other viruses, bacteria, gastric mucin, heat-inactivated fibroma suspensions, tumor suspensions, various animal sera, etc., have been added to heat-inactivated myxoma suspensions and injected into normal, hypersensitive, immunized, benzol-poisoned, etc., rabbits. Myxomatosis has never resulted.

An alternate interpretation to the one we have put forward, one which suggests that something in active fibroma virus "reactivates" the heat-inactivated myxoma virus and that transformation of fibroma virus into myxoma virus does not occur, has been advanced. The control studies outlined above indicate that, if this be true, nothing but active fibroma virus has served in this role. It should be pointed out, however, that these experiments do not disprove the alternate interpretation.

Another important question is this. can anything other than some heat-stable component derived from myxoma suspensions "transform" fibroma virus into myxoma virus? We have studied this question extensively. We have mixed other viruses, bacteria, gastric mucin, tumor extracts, animal sera, albumen, etc., with active fibroma virus and injected the mixtures into normal and "prepared" rabbits. "Preparation" has included poisoning with benzol, injuring by x-rays, various immunization procedures, etc. In no instance has

myxomatosis resulted. To date, therefore, only heat-inactivated myxoma suspensions, when mixed with active fibroma virus and injected into rabbits, have given rise to Infectious Myxomatosis

The best interpretation of these findings, we believe, postulates that fibroma virus and myxoma virus are closely related in their antigenic make-up, that the more virulent myxoma virus is antigenically the more complex, and that something in suspensions of myxomatous material, thermostable up to 75° C., which by itself is unable to induce myxomatosis in rabbits, lends virulence to fibroma virus, and changes it into myxoma virus

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SPECIES RELATIONSHIPS IN ONAGRA ¹

RALPH E. CLELAND

(Read in part, April 18, 1935)

ABSTRACT

Genoms or gene complexes with segmental arrangements of the California type exist, to an extent as yet unknown, in other regions than California. These are associated in most forms with complexes which are not of the California type. In order to learn the extent to which California complexes have permeated into regions distant from California, and also to discover whether non-California complexes fall into clearly recognizable groups from the standpoint of segmental arrangement, data must be accumulated with reference to the segmental arrangement of complexes which reside in regions other than California.

To this end, a large number of hybrids involving non-California complexes have been studied, and the segmental arrangements of their complexes determined as far as possible. Detailed reasoning is presented by means of which these determinations have been made. As a result of such analyses, it is suggested that *rigens* (of *muricata*) and *fascians* (of *ostrea*) are very closely related, that *gaudens* (of *lamarckiana*) and *rubens* (of the European *biennis*) show some indication of relationship, on the one hand to *rigens* and *fascians*, and on the other hand to *maculans* (of *skulliana*) and *accelerans* (of *oakesiana*). Furthermore, α Iowa 6 and β Iowa 6, while quite unrelated to each other in segmental arrangement, nevertheless both show a moderate approach in this respect to the California type of complex, suggesting that both are derived, by different lines of evolution, from the latter group. β Iowa 6 shows a close relationship to *elongans* (of *cockerelli*), and α Iowa 6 may be related in some degree to *maculans*. ²*Argillicola* shows a close relationship to the California complexes, a more distant affinity with the *curvans* type of complex. Lists of new chromosome configurations and of segmental arrangements are given in the tables, and the appendix contains brief descriptions of most of the hybrids included in this study.

In most Onagras, the mode of inheritance is peculiar, in that all or most of the genes received from one parent separate from those received from the other parent, and pass into different germ cells, and therefore into different progeny. A given bloc of genes, or a gene complex, as it is called, is thus transmitted from generation to generation intact, without admixture with genes from other blocs.

But while complexes are transmitted intact as a rule, occasional exchanges of material may occur between the various

¹ Supported by a grant from the Penrose Fund of the American Philosophical Society. Technical assistance has been rendered by Dr. B. L. Hammond.

chromosomes of a complex, or between non-homologous chromosomes of associated complexes. This phenomenon of segmental interchange has been an outstanding feature of *Onagra* evolution, and has resulted in very different arrangements of chromosomal material in different races. Now, there seems to be strong reason to believe that gene complexes which have had a relatively recent common origin are similar in the arrangement of chromosomal material, and vice versa, a fact that apparently gives us a ready means of determining, at least roughly, the degree of relationship between complexes, and hence between the races of which these complexes are components

Realizing, therefore, the probable phylogenetic importance of this fact, the author began a few years ago a study of the relationships among the wild *Onagras*, as these might be revealed through an analysis of the arrangements of their chromosomal materials. This work began with the California *Onagras* and resulted in the discovery, reported in 1934, (1) that the *Onagras* of California constitute a closely knit group, characterized by a particular type of segmental arrangement; (2) that genomes or gene complexes with segmental arrangements of the California type exist, to an extent as yet unknown, in other regions than California, (3) that gene complexes which are not of the California type (and these apparently constitute the bulk of those found east of the Rockies) are varied in character, possessing a great diversity of segmental arrangement. These studies raised certain important questions, including the following: (a) To what extent have complexes of the California type permeated into regions distant from California, and by what means have they reached these regions? (b) Is there evidence of relationship between non-California complexes; do they tend to fall into groups from the standpoint of segmental arrangement; is there therefore any evidence as to where the non-California types of genome have had their origin? An answer to these questions awaits the accumulation of data relative to the segmental arrangements of complexes which exist in other regions than

TABLE 1

NEW CHROMOSOME CONFIGURATIONS IN *ENOTHERA*

Species or Cross	Complex-combination	Chromosome-configuration
<i>argillicola</i> (fr Huntingdon, Pa.)	^h <i>argillicola</i> ^h <i>argillicola</i>	7 pairs (2 pls)
"Iowa 6"	α Iowa 6 β Iowa 6	O14
<i>argillicola</i> \times <i>crucata</i>	^h <i>argillicola</i> <i>flectens</i>	O4, O4, O6 (1 pl.)
<i>argillicola</i> \times <i>r-lamarckiana</i>	^h <i>argillicola</i> <i>gaudens</i>	O14 (1 pl)
<i>argillicola</i> \times <i>oakesiana</i>	^h <i>argillicola</i> <i>denudans</i>	O4, O10 (1 pl)
<i>argillicola</i> \times <i>ostrea</i>	^h <i>argillicola</i> β <i>ostrea</i>	O4, O6 (3 pls)
<i>blandina</i> \times <i>grandiflora</i>	^h <i>blandina</i> <i>acuens</i>	O4, O4 (3 pls)
	^h <i>blandina</i> <i>truncans</i>	O12 (3 pls)
<i>blandina</i> \times <i>suaveolens</i>	^h <i>blandina</i> <i>flavens</i>	O4, O6 (3 pls)
<i>chicaginensis</i> \times <i>blandina</i>	<i>excellens</i> ^h <i>blandina</i>	O4 (3 pls.)
<i>chicaginensis</i> \times <i>cockerelli</i>	<i>excellens</i> <i>elongans</i>	O4, O4, O4 (1 pl)
<i>chicaginensis</i> \times <i>grandiflora</i> (metacline)	<i>punctulans</i> <i>acuens</i>	O10 (1 pl)
<i>cockerelli</i> \times <i>chicaginensis</i>	<i>curtians</i> <i>punctulans</i>	O10 (3 pls)
<i>cockerelli</i> \times <i>grandiflora</i>	<i>curtians</i> <i>acuens</i>	O12 (1 pl)
	<i>curtians</i> <i>truncans</i>	*O14 (2 pls)
<i>cockerelli</i> \times "Johansen"	<i>curtians</i> ^h <i>Johansen</i>	O4, O6 (3 pls)
<i>cockerelli</i> \times <i>r-lamarckiana</i>	<i>curtians</i> <i>gaudens</i>	O14 (3 pls)
"Devil's Gate" \times "Iowa 6"	^h Dev G β Iowa 6	O4, O4, O4 (3 pls)
<i>erythrina</i> \times <i>r-lamarckiana</i>	^h <i>decipiens</i> <i>velans</i>	O6 (2 pls)
<i>erythrina</i> \times <i>suaveolens</i>	^h <i>decipiens</i> <i>flavens</i>	O4, O4 (1 pl)
	<i>velans</i> <i>flavens</i>	O4, O4 (3 pls)
<i>franciscana</i> de V \times <i>blandina</i>	^h <i>franciscana</i> ^h <i>blandina</i>	O6 (2 pls)
(<i>franc</i> de V \times <i>franc</i> E + S) \times "Iowa 6"	<i>franciscana</i> de V β Iowa 6	O4, O8 (2 pls)
	^h <i>franciscana</i> E + S β Iowa 6	O4, O4, O4 (2 pls)
<i>grandiflora</i> \times <i>argillicola</i>	<i>acuens</i> ^h <i>argillicola</i>	O4 (2 pls)
	<i>truncans</i> ^h <i>argillicola</i>	O12 (3 pls.)
<i>grandiflora</i> \times <i>chicaginensis</i>	<i>acuens</i> <i>punctulans</i>	O10 (2 pls.)
	<i>truncans</i> <i>punctulans</i>	O10 (2 pls)
<i>grandiflora</i> \times <i>cockerelli</i>	<i>acuens</i> <i>elongans</i>	O4, O4 (2 pls)
	<i>truncans</i> <i>elongans</i>	O12 (1 pl)
<i>grandiflora</i> \times "Iowa 6"	<i>acuens</i> β Iowa 6	O4, O4 (3 pls.)
	<i>truncans</i> β Iowa 6	O4, O8 (3 pls.)
	<i>acuens</i> α Iowa 6	O6, O6 (1 pl)
<i>grandiflora</i> \times <i>muricata</i>	<i>truncans</i> <i>curvans</i>	O10 (3 pls.)
<i>grandiflora</i> \times <i>ostrea</i>	<i>truncans</i> β <i>ostrea</i>	O12 (3 pls)
<i>grandiflora</i> \times <i>skulliana</i>	<i>acuens</i> <i>maculans</i>	O10 (1 pl)
	<i>truncans</i> <i>maculans</i>	O14 (4 pls)
	<i>jugens</i> <i>acuens</i>	O8 (1 pl)
	<i>jugens</i> <i>truncans</i>	O14 (2 pls)
<i>grandiflora</i> \times <i>suaveolens</i>	<i>acuens</i> <i>flavens</i>	*O4 (1 pl)
	<i>truncans</i> <i>flavens</i>	*O14 (1 pl)
<i>hookeri</i> \times <i>erythrina</i>	^h <i>hookeri</i> ^h <i>decipiens</i>	O4 (7 pls)
"Iowa 6" \times "Devil's Gate"	α Iowa 6 ^h Dev G.	O4, O6 (2 pls)
"Iowa 6" \times <i>franciscana</i> Sh.	α Iowa 6 ^h <i>franciscana</i>	O4, O8 (3 pls)

TABLE 1 (continued)

Species or Cross	Complex-combination	Chromosome-configuration
"Iowa 6" × <i>grandiflora</i>	<i>α Iowa 6 acuens</i>	06, 06 (2 pls.)
	<i>α Iowa 6 truncans</i>	04, 010 (2 pls.)
"Iowa 6" × <i>shulliana</i>	<i>α Iowa 6 maculans</i>	04, 04 (3 pls.)
	<i>α Iowa 6 jugens</i>	014 (3 pls.)
<i>r-lamarckiana</i> × <i>argillicola</i>	<i>velans</i> ^b <i>argillicola</i>	010 (3 pls.)
<i>r-lamarckiana</i> × <i>blandina</i>	<i>gaudens</i> ^b <i>blandina</i>	010 (3 pls.)
	<i>velans</i> ^b <i>blandina</i>	08 (3 pls.)
<i>r-lamarckiana</i> × <i>cockerelli</i>	<i>velans elongans</i>	04, 06 (1 pl.)
	<i>gaudens elongans</i>	014 (1 pl.)
<i>r-lamarckiana</i> × <i>erythrina</i>	<i>velans</i> ^b <i>decipiens</i>	06 (3 pls.)
	<i>gaudens</i> ^b <i>decipiens</i>	010 (1 pl.)
<i>r-lamarckiana</i> × "Iowa 6"	<i>velans β Iowa 6</i>	04, 08 (3 pls.)
	<i>gaudens β Iowa 6</i>	014 (2 pls.)
<i>r-lamarckiana</i> × <i>shulliana</i>	<i>gaudens maculans</i>	04, 06 (2 pls.)
	<i>velans maculans</i>	012 (2 pls.) (confirmation of Sturtevant '31)
<i>muricata</i> × <i>argillicola</i>	<i>rigens</i> ^b <i>argillicola</i>	014 (1 pl.)
<i>muricata</i> × <i>blandina</i>	<i>rigens</i> ^b <i>blandina</i>	08 (3 pls.)
<i>muricata</i> × <i>cockerelli</i>	<i>rigens elongans</i>	04, 010 (2 pls.)
<i>muricata</i> × <i>erythrina</i>	<i>rigens</i> ^b <i>decipiens</i>	06 (1 pl.)
<i>muricata</i> × <i>grandiflora</i>	<i>rigens acuens</i>	04, 08
	<i>rigens truncans</i>	014
	<i>curvans acuens</i>	06, 04
<i>muricata</i> × <i>r-lamarckiana</i>	<i>rigens velans</i>	08
<i>muricata</i> × <i>oakesiana</i>	<i>rigens denudans</i>	014 (1 pl.)
<i>muricata</i> × <i>ostrea</i>	<i>rigens β ostrea</i>	014 (3 pls.)
<i>nobska</i> × "Iowa 6"	<i>anesceus β Iowa 6</i>	014 (2 pls.)
	<i>pubens β Iowa 6</i>	014 (2 pls.)
	<i>pubens α Iowa 6</i>	012 (2 pls.)
<i>nobska</i> × <i>ostrea</i>	<i>anesceus β ostrea</i>	014 (3 pls.)
<i>nobska</i> × <i>shulliana</i>	<i>pubens jugens</i>	04, 08 (3 pls.)
	<i>pubens maculans</i>	012 (3 pls.)
<i>ostrea</i> × (<i>bland</i> × <i>suaveolens</i>)	<i>fascians flavens</i>	04, 06 (2 pls.)
	<i>fascians</i> ^b <i>blandina</i>	08 (2 pls.)
<i>ostrea</i> × <i>franciscana</i> Sh	<i>fascians</i> ^b <i>franciscana</i>	06 (2 pls.)
<i>ostrea</i> × <i>grandiflora</i>	<i>fascians acuens</i>	04, 08 (3 pls.)
	<i>fascians truncans</i>	014 (3 pls.)
<i>ostrea</i> × "Iowa 6"	<i>fascians β Iowa 6</i>	014 (2 pls.)
<i>ostrea</i> × (<i>r-lam.</i> × <i>blandina</i>)		
<i>lata</i>	<i>fascians</i> ^b <i>blandina</i>	08 (3 pls.)
	<i>fascians gaudens</i>	06 (1 pl.)
<i>ostrea</i> × <i>nobska</i>	<i>fascians anesceus</i>	014 (5 pls.)
<i>shulliana</i> × (<i>bland</i> × <i>suav</i>)	<i>jugens</i> ^b <i>blandina</i>	012 (3 pls.)
	<i>jugens flavens</i>	010 (1 pl.)
	<i>maculans</i> ^b <i>blandina</i>	010 (2 pls.)
	<i>maculans flavens</i>	04, 06 (1 pl.)

TABLE 1 (continued)

Species or Cross	Complex-combination	Chromosome-configuration
<i>shulliana</i> × <i>franciscana</i> Sh	<i>jugens</i> ^b <i>franciscana</i>	O12 (3 pls)
	<i>maculans</i> ^b <i>franciscana</i>	O10 (3 pls)
<i>shulliana</i> × <i>grandiflora</i>	<i>jugens</i> <i>acuens</i>	O8 (4 pls)
	<i>jugens</i> <i>truncans</i>	O14 (2 pls)
	<i>maculans</i> <i>acuens</i>	O10 (1 pl)
	<i>maculans</i> <i>truncans</i>	O14 (2 pls)
<i>shulliana</i> × "Iowa 6"	<i>jugens</i> β Iowa 6	O4, O6 (2 pls)
	<i>jugens</i> α Iowa 6	O14 (1 pl)
<i>shulliana</i> × <i>r-lamarckiana</i>	<i>jugens</i> <i>gaudens</i>	O14 (confirmation of Sturtevant '31)
	<i>maculans</i> <i>gaudens</i>	O4, O6 (1 pl)
	<i>jugens</i> <i>velans</i>	O12 (2 pls) (confirmation of Sturtevant '31)
<i>shulliana</i> × <i>muricata</i>	<i>jugens</i> <i>curvans</i>	O10 (3 pls)
<i>shulliana</i> × <i>nobisla</i>	<i>jugens</i> <i>anescens</i>	O10 (4 pls)
<i>shulliana</i> × <i>oakesiana</i>	<i>jugens</i> <i>denudans</i>	O10 (4 pls)
<i>suaveolens</i> × <i>grandiflora</i>	^a <i>albicans</i> <i>acuens</i>	O10 (3 pls)
	^a <i>albicans</i> <i>truncans</i>	O12 (2 pls)
	<i>flavens</i> <i>truncans</i>	O14 (4 pls)

^a F₂ of this cross studied cytologically by Gerhard (1929), and has same configuration as F₁

California. Consequently, a large number of hybrids involving non-California complexes have been studied during the past season, in order further to analyze the segmental arrangements of these complexes. The results of this study are embodied in the present paper.

1. DATA

A list of chromosome configurations in such hybrids and new forms as have hitherto been unreported will be found in table 1. Brief descriptions of most of these cultures will be found in the appendix.

In table 2 (p. 482) will be found the results of analyses of the segmental arrangements of various genomes present in these hybrids, indicating the extent to which their analysis has been carried. Each pair of numerals connected by a dot represents a chromosome; corresponding ends of chromosomes are represented by the same numeral. The different arrange-

ments of the numerals indicate the different arrangements of chromosomal material in the various complexes. Those chromosomes which are bold face represent determinations or postulations made during the season 1934-5 In order, there-

TABLE 2
SEGMENTAL ARRANGEMENTS OF CERTAIN COMPLEXES OF ONAGRA

<i>hookeri</i>	1 2	3 4	5 6	7 8	9 10	11 12	13 14
<i>flavens</i>	1 4	3 2	5 6	7 8	9-10	11-12	13 14
<i>vilans</i>	1 2	3 4	5 8	7 6	9 10	11-13	13 14
<i>franciscana</i> E & S	1 2	3 4	5 6	7 10	9 8	11 12	13 14
"N"	1 2	3 4	5 6	7 14	9 10	11 12	8 13
<i>acutus</i>	1 4	3 2	5 6	7 10	9 8	11 12	13 14
<i>rigens</i>	1-2	3 4	5 6	7 11	9 10	12 13	8 14
<i>fascians</i>	1 2	3 4	5 6	7 11	9 10	12 13	8 14
				7-10	9 12	8 11	13 14
<i>ablandina</i>	1-2	3 4	5-6	9 8	7-12	11 10	
				7 10	9 14	13 8	11 12
				7 14	9 8	13 10	
<i>decipiens</i>	1 2	3-4	5 6	9-10	7-12	8 11	13 14
					7-14	8 13	11-12
			5 8	9 6	7 14	13 10	11 12
<i>elongans</i>	1 4	3 2	5 10	7 6	7 12	11 10	13 14
					9 12	8 11	13 14
					9 14	11-12	13 8
<i>curians</i>		3-4				11 12 or 13 14	
					11 12	5 13	6 14
<i>stringens</i>	1-4	3 2	7-8	9 10	13 14	5 14	6 13
						5-11	6 12
						5 12	6 11
<i>Iowa</i> 6 α (♀)	1 2 or 3 4		7 10 or 9 8			11-12 or 13 14	
<i>Iowa</i> 6 β (♂)	1 4	3 2				12 13	8 14)
<i>gaudens</i> (and <i>rubens</i>)	1 2		5-6	2 of (7-11			
<i>maculans</i>	1 2		5 6	7-10 or 9-8			
<i>jugens</i>	1 4 or 3 2			7 10	8 13	11 12	
				9 8	7-14		
<i>albicans</i>	1 4			8 13	7 10		
				7 14	9 8		
<i>accelerans</i>			5 6 or	(1-4 or 3 2 with	7-14	9 8)	
					7 10	13-8)	
<i>pubens</i>			5 6 or 7 8				
<i>punctulans</i>	1 4		7 8			11 12 or 13 14	
<i>curvans</i>		3 2		7 10 or 9-8			
<i>flectens</i> (Renner)	1 4	3 2	1 of (7 11			12 13	8-14)
(Waterbury)	1 4 or 3 2						
	1 4	3-5	2 6			4	
		3 6	2 5	7 10	9 8	11-12	13-14
		1-5	4 6				
<i>argulicola</i>	3 2	1-6	4 5				

fore, to compare what has been learned this season with what was previously known regarding the segmental arrangement of the complexes tested, it is only necessary to compare the bold face chromosomes with those which are not bold face. It will be seen that a considerable advance has been made during the year in the analysis of the distribution of chromosomal material within these particular complexes.

We will now present the reasoning which has led to the determinations listed in table 2. (The segmental arrangements of certain genomes which have previously been fully analyzed are included in the table, as they enter into the reasoning. Furthermore, certain complexes are included which are found in mutants or in forms growing in Europe, since these also are of importance in the reasoning.)

(1) *Rigens* (egg complex of *muricata*, a European form)

- rigens* ^h*hookeri* = 06, 4 pairs ¹
- rigens* *flavens* = 04, 06, 2 pairs
- rigens* *velans* = 08, 3 pairs
- rigens*·*acuens* = 04, 08, 1 pair
- rigens*·*rubens* = 06, 4 pairs

Rigens gives 2 more pairs with ^h*hookeri* than with *flavens*. It therefore must have from the standpoint of segmental arrangement 2 chromosomes which are common to ^h*hookeri* but not to *flavens*. Since the only ^h*hookeri* chromosomes which are not in *flavens* are 1 2, 3 4, these must be the chromosomes in question. *Rigens* gives one more pair with ^h*hookeri* than it does with *velans*. It therefore must have one of the ^h*hookeri* chromosomes ² not present in *velans*, namely, 5 6 or 7 8. (a) If it has 5·6, and not 7·8, it already has a chromosome in common with *acuens* (5·6) and cannot therefore have 11·12 or 13·14, since it can have no other chromosome in common with *acuens*. On the other hand, since it cannot have

¹ The lists of configurations presented in the text include only such determinations (new and old) as are of use in the arguments herein presented. Most of the complexes discussed have been studied in many additional combinations.

² It is obvious that expressions such as this refer only to segmental arrangement, and not to genetic composition. A chromosome common to 2 complexes in segmental arrangement is not necessarily genetically identical in these complexes.

7·8, 11·12, 13·14, it must have 9·10, in order to give 4 pairs with *^hhookeri*. If, therefore, *rigens* has 5·6, it must also have 9·10 (b) If it has 7·8, then it cannot have 5·6. It also cannot have 7·10 or 9·8 of *acuens* (having already 7·8). It must therefore have 11·12 or 13·14 to give one pair with *acuens*, and this will give the 4th pair with *^hhookeri*.

A choice between (a) and (b) can be made as a result of genetical, rather than cytological investigation. Renner has shown that *Sp* segregates independently in *rigens flavens* and *rigens rubens*, and 5·6 has previously been defined as the chromosome which carries *Sp* (Cleland and Blakeslee 1931, p. 220) The fact that *Sp* segregates in these combinations probably means that there is a pair of 5·6 chromosomes present, in other words, that *rigens* has 5·6. *Rigens*, then, has 1·2, 3·4, 5·6, 9·10.

The possibilities, then, for the *rigens* chromosomes which are in the O6 with *^hhookeri*, are (omitting duplication).

11	11	13	13
7 12	8 12	11·	12
13	14	14	14

(7·14 and 8·13 are impossible, since they would cause *rigens* to have too many pairs with "*N*," as defined) ¹

If *rigens* has 7·11, the *rigens*·*^hhookeri* circle will have to be as follows (*rigens* chromosomes bold face)

7·11—11·12—12·13—13·14—14·8—8·7
 (other choices impossible)
 (*rigens* will have 7·11 12·13 8·14)

If *rigens* has 7·12, the circle will have to be:

7 12—12·11—11·13—13·14—14·8—8·7
 (other choices impossible)
 (*rigens* will have 7·12 11·13 8·14)

¹ Sturtevant (1931) reports *fascians*·*N* to have O8, 3 pairs. His *fascians* differs from mine by but a single interchange. My *fascians* apparently has the same segmental arrangement as *rigens*. A *rigens*, however, differing by no more than one interchange from a complex giving O8 with *N*, would have to give at least O6 with *N*. *Rigens*·*N*, therefore, can have no more than 4 pairs of chromosomes.

If *rigens* has 7·13, the circle will have to be·

$$\begin{array}{c}
 14 \cdot 11 - 11 \quad 12 - 12 \quad 8 - 8 \cdot 7 \\
 \swarrow \quad \quad \searrow \\
 7 \quad 13 - 13 \cdot 14 \quad \text{or} \\
 \swarrow \quad \quad \searrow \\
 14 \cdot 12 - 12 \quad 11 - 11 \cdot 8 - 8 \cdot 7 \\
 \left(\text{rigens will have } 7 \cdot 13 \left\{ \begin{array}{ll} 8 \cdot 12 & 11 \quad 14 \\ 8 \cdot 11 & 12 \cdot 14 \end{array} \right. \right)
 \end{array}$$

Renner (1933) reasons on genetical grounds that *rigens* should have 13 12, and either 7·11 8·14 or 7 14 8 11. Our reasoning shows that a *rigens* with 13·12 must have 7·11 and 8·14, it also shows that 7·14 is impossible. There is but one choice left us, therefore, which conforms to the reasoning of Renner, namely 7·11, 12 13, 8 14. These are therefore defined as the chromosomes which constitute the *rigens* half of the *rigens* ^h*hookeri* circle of 6.

$$\text{Rigens} = 1 \quad 2 \quad 3 \cdot 4 \quad 5 \quad 6 \quad 7 \quad 11 \quad 9 \cdot 10 \quad 12 \cdot 13 \quad 8 \quad 14$$

- (11) *Fascians* (egg complex of *ostrea* from New England, the *fascians* of Emerson and Sturtevant apparently differs from ours by one segmental interchange. The configurations given below are those produced by our *fascians*).

$$\begin{array}{ll}
 \text{fascians } ^h\text{franciscana Sh} & = \text{O6, 4 pairs} \\
 \text{fascians flavens} & = \text{O4, O6, 2 pairs} \\
 \text{fascians acuens} & = \text{O4, O8, 1 pair}
 \end{array}$$

Fascians gives 2 more pairs with ^h*franciscana* Sh (same arrangement as ^h*hookeri*) than with *flavens*. It therefore must have the 2 *franciscana* chromosomes not present in *flavens*, namely, 1·2 3·4. It gives O4, O6 with *flavens* and O4, O8 with *acuens*. In both cases the O4 is due to the presence of 1·2 3·4 in *fascians*, the pair present in *fascians flavens* and not in *fascians acuens* is due to the presence in *fascians* of either 7·8 or 9·10, which are present in *flavens*, but not in *acuens*.

The possibilities for *fascians* cannot as yet be further analyzed on the basis of available information with respect to

segmental arrangements. However, our *fascians* and *rigens* have been studied in combination with 7 other segmental arrangements (*flavens*, *acuens*, ^h*hookeri* or ^h*franciscana* Sh., ^h*Johansen* or ^h*Dalton*, ^h*blandina*, *rubens* or *gaudens*, β *ostreae*). In each one of these cases, *fascians* and *rigens* have agreed in the configuration of chromosomes which they have produced, and in no case have they failed to agree. There is a strong likelihood, therefore, that *fascians* and *rigens* have the same arrangement of segments, and we will assume for the present that this is the case.

(iii) ^h*Blandina* (genom in homozygous *blandina*, mutant from *lamarckiana*)

^h <i>blandina</i> · ^h <i>hookeri</i>	= 06, 4 pairs
^h <i>blandina</i> · <i>flavens</i>	= 04, 06, 2 pairs
<i>excellens</i> ^h <i>blandina</i>	= 04, 5 pairs
<i>velans</i> · ^h <i>blandina</i>	= 08, 3 pairs
<i>rigens</i> · ^h <i>blandina</i>	= 08, 3 pairs
^h <i>blandina</i> · <i>acuens</i>	= 04, 04, 3 pairs

^h*Blandina* gives 4 pairs with ^h*hookeri* and only 2 pairs with *flavens*. It therefore has 1·2 3·4. It gives 2 more pairs with *excellens* than with *velans*, and therefore has 2 *excellens* chromosomes not present in *velans*. These must be 2 of 5·6, 7·10, 9·8. It gives one more pair with *acuens* than with *flavens*, and so has one *acuens* chromosome not present in *flavens*. This must be 7·10 or 9·8. Since it cannot have both 7·10 and 9·8, and yet must have 2 of 5·6, 7·10, 9·8, it must definitely have 5·6, and either 7·10 or 9·8. ^h*Blandina* gives 3 pairs with *velans*. Two of these are 1·2 and 3·4. The third cannot be 5·8 or 7·6, since it already has 5·6. Nor can it be 9·10, since ^h*blandina* already has 7·10 or 9·8. So ^h*blandina* has 11·12 or 13·14. Using *rigens* as antagonist, which gives 08 with ^h*blandina*, and arranging all possible choices for ^h*blandina* with the chromosomes of *rigens*, we find but 4 possibilities for the last 4 chromosomes of ^h*blandina*, as follows:

$$^h\textit{blandina} = 1 \cdot 2 \quad 3 \cdot 4 \quad 5 \quad 6 \quad \left\{ \begin{array}{lll} 7 \cdot 10 & 9 \cdot 12 & 8 \cdot 11 \\ 7 \cdot 12 & 9 \cdot 8 & 11 \cdot 10 \\ 7 \cdot 10 & 9 \cdot 14 & 13 \cdot 8 \\ 7 \cdot 14 & 9 \cdot 8 & 13 \cdot 10 \end{array} \right\} \begin{array}{l} 13 \cdot 14 \\ \\ \\ 11 \cdot 12 \end{array}$$

The first 2 of these will give 08 with "*N*," the latter 2 will give 04 with "*N*." The possibilities will be reduced to 2 as soon as the configuration of *^hblandina*·"*N*" has been determined. A further genetical test is also available. Renner has defined 11·12 as the chromosome containing *def*, a gene in *flavens* for defective petals. If *flavens*·*^hblandina* segregates for defective petals it will eliminate the first 2 possibilities, as it will mean that 11·12 is present as a pair instead of being involved in the 06 in this hybrid.

(iv) *^hDecipiens* (alethal genom of *erythrina*, mutant from *lamarchiana*)

$$\begin{array}{ll} ^h\textit{hookeri} \cdot ^h\textit{decipiens} & = 04, 5 \text{ pairs} \\ ^h\textit{decipiens} \cdot \textit{flavens} & = 04, 04, 3 \text{ pairs} \\ ^h\textit{decipiens} \cdot \textit{velans} & = 06, 4 \text{ pairs} \\ \textit{rigens} \cdot ^h\textit{decipiens} & = 06, 4 \text{ pairs} \end{array}$$

^hDecipiens gives 5 pairs with *^hhookeri*, and only 3 pairs with *flavens*. It therefore has 1·2 3·4. It gives one fewer pair with *velans* than with *^hhookeri*, and therefore has 5 6 or 7·8 (one of the 2 *^hhookeri* chromosomes not in *velans*). In order to give 5 pairs with *^hhookeri*, it must have 2 of the last 3 *^hhookeri* chromosomes, i.e., 2 of 9·10, 11·12, 13·14. If it has 7 8, and not 5·6, then it cannot give 4 pairs with *rigens*, for it cannot have 7·11 or 8·14 (having 7·8), and since it must have 11·12 or 13·14, and cannot therefore have 12·13, there are not enough *rigens* chromosomes left with which *^hdecipiens* can pair, unless it has both 9·10 and 5·6, in which case, however, 7·8 is impossible. It cannot therefore have 7·8, and must have 5·6 9·10. The possibilities for the remaining 3 chromosomes are as follows: (a) if it has 13·14, the other 2 chromosomes may be 7·12 8·11 or 7·11 8·12. The latter is impossible, as it would give too many pairs with *rigens*; (b) if *^hdecipiens* has 11·12, the remaining chromosomes may be 7·14

8·13 or 7·13 8·14. The latter is impossible as it also would give too many pairs with *rigens*. Only 2 possibilities remain for ^h*decipiens*, namely:

$$^h\textit{decipiens} = 1 \cdot 2 \quad 3 \quad 4 \quad 5 \quad 6 \quad 9 \cdot 10 \quad \left\{ \begin{array}{l} 7 \cdot 12 \quad 8 \cdot 11 \quad 13 \cdot 14 \\ 7 \cdot 14 \quad 8 \cdot 13 \quad 11 \cdot 12 \end{array} \right.$$

It will be possible to choose between these by combining ^h*decipiens* with "N". If ^h*decipiens*·"N" has 7 pairs, the second alternative is correct; if it has 06, the other alternative is correct. An additional check will be available after it is learned whether ^h*blandina* has 11·12 or 13·14, for then it will be possible to choose between the ^h*decipiens* possibilities by combining ^h*decipiens* and ^h*blandina*.

(v) *Elongans* (pollen complex of *cockerelli*, from Colorado)

^h <i>hookeri</i> · <i>elongans</i>	= 04, 08, 1 pair
<i>flavens</i> · <i>elongans</i>	= 08, 3 pairs
<i>velans</i> · <i>elongans</i>	= 04, 06, 2 pairs
^h <i>franciscana</i> E + S. <i>elongans</i>	= 04, 04, 04, 1 pair
<i>rigens</i> · <i>elongans</i>	= 04, 010

Elongans gives 3 pairs with *flavens* and only 1 pair with ^h*hookeri*. It has therefore the 1 4 3·2 of *flavens*. It gives 1 more pair with *velans* than with ^h*hookeri*, and therefore has a *velans* chromosome not found in ^h*hookeri*, i.e., 5·8 or 7·6. If it has 5 8, then it must have 9·6, in order to complete a 04 with *franciscana* E & S. If it has 7·6, then it must have 5·10 for the same reason. Since it must have 9 6 or 5·10, it cannot have 9·10; in order, therefore, to give a pair with ^h*hookeri*, and the second pair with *velans*, it must have 11·12 or 13·14. Using *rigens* as antagonist (which gives 04, 010 with *elongans*, the 010 involving the last 5 chromosomes), it is possible by testing the possibilities for the 010 to show that only 4 possibilities remain for the *elongans* arrangement. To illustrate the method, one possibility will be worked out in detail. Beginning with 5·8 of *elongans*, the *rigens* chromosomes which will unite with this chromosome are 6·5 and 8·14. To 6 5 will unite the 6·9 of *elongans*, and to this in turn the 9·10

of *rigens*. So far, we have the following chain of 7 (*elongans* chromosomes bold face): 7·10—10·9—9·6—6·5—5·8—8·14—14·7. Supposing *elongans* to have 11·12, this will be joined by 7·11 at one end and 12·13 at the other, giving the following chain of 3: 7·11—11·12—12·13. It is therefore only necessary to decide which end of the chain of 3 unites with a given end of the chain of 7 to have the completed circle. If 12·13 joins the right hand end of the long chain, the latter will need to have as its end chromosome 14·13, which *elongans* cannot have if it has 11·12. Consequently, 12·13 must join the left hand end of the long chain, in which case the left end chromosome will be 13·10 and the right end chromosome will be 14·7. The entire chain or circle of 10 therefore is (*elongans* chromosomes bold face).

12·13—13 10—10·9—9 6—6·5—5 8—8 14—14 7—7 11
—11 12

Elongans would then have 1 4 3·2 5 8 9·6 7·14 13 10 11 12 (gives O₄, O₆ with "N")

The other possibilities, which may be similarly worked out, are:

1 4	3 2	5 8	9 6	7 12	11 10	13 14	(gives O ₄ , O ₁₀ with "N")
1·4	3 2	5 10	7 6	9 12	8 11	13 14	(" O ₄ , O ₁₀ " ")
1 4	3 2	5 10	7 6	9·14	11·12	13·8	(" O ₄ , O ₆ " ")

One can eliminate 2 of these possibilities by crossing *elongans* with "N." If the hybrid has O₄, O₆, *elongans* has 11·12 (possibilities 1 and 4), if it has O₄, O₁₀, *elongans* has 13 14 (possibilities 2 and 3). There is a likelihood that these possibilities may be still further reduced by crossing *elongans* with *^Adecipiens* and *^Ablandina*.

(vi) *Curtans* (egg complex of *cockerelli*)

<i>curtans</i> · <i>^Ahookeri</i>	=	O ₁₀ , 2 pairs
<i>curtans</i> · <i>flavens</i>	=	O ₁₂ , 1 pair
<i>curtans</i> · <i>gaudens</i>	=	O ₁₄
<i>curtans</i> · <i>^AJohansen</i>	=	O ₄ , O ₆ , 2 pairs

Curtans gives one more pair with ^h*hookeri* than with *flavens*. It must therefore have 1·2 or 3·4, not both. It gives ⊙14 with *gaudens*, and therefore cannot have 1·2. It must therefore have 3·4. *Curtans* has one of the last 5 chromosomes of ^h*hookeri*. This cannot be 7·8 or 9·10, for the following reason: 7·10 and 9·8 of ^h*Johansen* must be in different circles in *curtans*·^h*Johansen* in order that *curtans*·^h*hookeri* may have ⊙10 and *curtans*·^h*Johansen* ⊙4, ⊙6 (the correct configuration). But either 7·8 or 9·10 would tie 7·10 and 9·8 of ^h*Johansen* into the same circle in *curtans*·^h*Johansen*. *Curtans* cannot, therefore, have 7·8 or 9·10, and so must have 5·6 or 11·12 or 13·14. It cannot have 5·6, however, since it gives ⊙14 with *gaudens*.

$$\textit{curtans} = 3 \cdot 4 \quad 11 \cdot 12 \text{ or } 13 \cdot 14$$

If *elongans* has 11·12, *curtans* has 13·14 and v·v.

(vii) *Stringens* (pollen complex of *strigosa*)

^h*hookeri*·*stringens* = ⊙4, ⊙4, 3 pairs (prediction)

flavens·*stringens* = ⊙4, 5 pairs

gaudens·*stringens* = ⊙14

acuens·*stringens* = ⊙4, ⊙4, 3 pairs

Stringens gives 2 more pairs with *flavens* than with ^h*hookeri*. It therefore has 1 4 3·2 (Emerson + Sturtevant, 1931, Cleland + Blakeslee, 1931). It gives ⊙14 with *gaudens* and therefore does not have 5·6. It gives 2 more pairs with *flavens* than with *acuens*, and must therefore have the 2 *flavens* chromosomes not present in *acuens*, namely 7·8 9·10. The second circle with *acuens* must include 5·6 of *acuens*, since this chromosome is not present in *stringens*. Therefore this circle can only include one of 11·12, 13·14, and *stringens* must have one of these chromosomes common to *acuens*. If it has 11·12, the possibilities for the *stringens* chromosomes in the second *acuens*·*stringens* circle are 5·13 6·14 or 5·14 6·13. If it has 13·14, the possibilities are 5·11 6·12 or 5·12 6·11.

$$stringens = 1 \ 4 \ 3 \cdot 2 \ 7 \cdot 8 \ 9 \cdot 10 \left\{ \begin{array}{l} 11 \cdot 12 \left\{ \begin{array}{l} 5 \cdot 13 \ 6 \cdot 14 \\ 5 \cdot 14 \ 6 \cdot 13 \end{array} \right. \\ 13 \cdot 14 \left\{ \begin{array}{l} 5 \ 11 \ 6 \cdot 12 \\ 5 \cdot 12 \ 6 \cdot 11 \end{array} \right. \end{array} \right.$$

(When the correct alternative for ^h*decipiens* is determined, it will be possible to tell whether *stringens* has 11·12 or 13·14 by crossing it with ^h*decipiens*.)

(viii) α *Iowa* 6 (egg complex of “*Iowa* 6,” occasionally transmitted through pollen)

α *Iowa* 6·^h*Devil's Gate* = 04, 06, 2 pairs

α *Iowa* 6 *acuens* = 06, 06, 1 pair

α *Iowa* 6 ^h*franciscana* Sh. = 04, 08, 1 pair

α *Iowa* 6 gives 2 pairs with ^h*Devil's Gate* and 1 pair with *acuens*. It therefore has one ^h*Devil's Gate* chromosome not present in *acuens*, which must be 1·2 or 3·4. It cannot have both of these. It gives 2 pairs with ^h*Devil's Gate* and 1 pair with ^h*franciscana* Sh. It has therefore a ^h*Devil's Gate* chromosome not present in ^h*franciscana* Sh. This must be 7·10 or 9·8. The 2 pairs in α *Iowa* 6·^h*Devil's Gate* are thus provided for, and α *Iowa* 6 cannot have 5·6, 11·12, 13·14

$$\alpha \text{ } Iowa \ 6 = 1 \cdot 2 \text{ or } 3 \ 4 \ 7 \cdot 10 \text{ or } 9 \cdot 8$$

(ix) β *Iowa* 6 (pollen complex of “*Iowa* 6”)

acuens· β *Iowa* 6 = 04, 04, 3 pairs

^h*Devil's Gate*· β *Iowa* 6 = 04, 04, 04, 1 pair

^h*franciscana* de V· β *Iowa* 6 = 04, 08, 1 pair

velans· β *Iowa* 6 = 04, 08, 1 pair

β *Iowa* 6 gives 3 pairs with *acuens*, and only 1 pair with ^h*Devil's Gate*. It therefore has 2 *acuens* chromosomes not present in ^h*Devil's Gate*. These must be 1·4 3·2. It gives one pair with ^h*franciscana* and *velans* and has therefore one of the last 5 chromosomes of each. The 5·6 7·8 of ^h*franciscana* and the 5·8 7·6 of *velans* are mutually exclusive. If it had 5·8 or 7·6 in common with *velans*, it would not have 5·6 or

7·8 and would need to have 9·10 or 11·12 or 13·14 in common with *^hfranciscana*. But *velans* also has these, which would give β Iowa 6 too many pairs with *velans*. The reverse argument is true if we assume β Iowa 6 has 5·6 or 7·8. It must therefore have one of 9·10, 11·12, 13·14. It cannot have 7·10 or 9·8 of *acuens*, for if it has either of these, both 11·12 and 13·14 would have to be involved in circles of 4 with *acuens* and could not therefore be present in β Iowa 6. That would leave only 9·10 to pair with *^hfranciscana*. But β Iowa 6 could not have 9·10 if it already has 7·10 or 9·8, as these are mutually exclusive. Hence β Iowa 6 cannot have 7·10 or 9·8. Since therefore β Iowa 6 cannot have 7·10 or 9·8; since furthermore it must have one of the last 5 *^hDevil's Gate* chromosomes, and cannot have 5·6, it must have 11·12 or 13·14. It cannot therefore have 9·10 since it has but 1 of the last 5 chromosomes of *^hhookeri*. β Iowa 6 has its segments so arranged that one circle of 4 with *acuens* includes 7·10 of *acuens*, the other includes 9·8. These chromosomes have in β Iowa 6 exchanged, the one with either 5·6 or 11·12 or 13·14, the other with 1 of the same 3 chromosomes not involved in the first exchange

$$\beta \text{ Iowa } 6 = 1 \cdot 4 \quad 3 \cdot 2 \quad 11 \cdot 12 \text{ or } 13 \cdot 14$$

(x) *Gaudens* (a genom of *lamarckiana*) and *rubens* (a genom of *biennis*)

<i>gaudens</i> · <i>velans</i>	= 012, 1 pair
<i>rubens</i> · <i>velans</i>	= 012, 1 pair
<i>fascians</i> · <i>gaudens</i>	= 06, 4 pairs
<i>rigens</i> · <i>rubens</i>	= 06, 4 pairs

Gaudens and *rubens* give identical configurations in each case in which they have been both studied with the same antagonist. They have, therefore, been assumed to have the same segmental arrangement. They have previously been assigned 1·2 and 5·6 on genetical grounds (Cleland + Blakeslee, 1931, Emerson + Sturtevant, 1931), since *R*, which segregates independently in *velans*·*gaudens*, is in 1·2, and *sp*, which splits independently in *rubens*·*velans*, is in 5·6. *Fascians*

gives 06 and 4 pairs with *gaudens*, and *rubens* gives 06 and 4 pairs with *rigens*. The *gaudens-rubens* segmental arrangement, therefore, has 4 chromosomes in common with the *fascians-rigens* arrangement. Two of these, of course, are 1·2 and 5·6. The others cannot be 3·4 or 9·10 of *rigens*, since these, being present in *velans*, cannot be present in *gaudens* or *rubens*. The remaining 2 chromosomes common to the 2 arrangements must be 2 of the following *fascians-rigens* chromosomes: 7·11, 12·13, 8·14.

$$\textit{gaudens} \text{ and } \textit{rubens} = 1 \cdot 2 \quad 5 \cdot 6 \quad \text{two of } \begin{cases} 7 \cdot 11 \\ 13 \cdot 12 \\ 8 \cdot 14 \end{cases}$$

(xi) *Maculans* (a genom of *shulliana*, more commonly transmitted through pollen)

^A <i>Mateo</i> · <i>maculans</i>	= 08, 3 pairs
<i>maculans</i> ^A <i>franciscana</i> Sh	= 010, 2 pairs
<i>velans</i> · <i>maculans</i>	= 012, 1 pair
<i>maculans</i> · <i>acuens</i>	= 010, 2 pairs
<i>maculans</i> "N"	= 012, 1 pair

Maculans gives 3 pairs with ^A*Mateo*, but 2 with ^A*franciscana* Sh. It therefore has a ^A*Mateo* chromosome not present in ^A*franciscana* Sh., namely, 7·10 or 9·8. It gives 2 pairs with *franciscana* Sh. and 1 pair with *velans*, and must therefore have a ^A*franciscana* chromosome not present in *velans*, i.e., 5·6 or 7·8. It cannot, however, have 7·8, since it has just been shown that it must have 7·10 or 9·8. It therefore has 5·6. Since it gives 3 pairs with ^A*Mateo* and but 2 pairs with *acuens*, it has a ^A*Mateo* chromosome not found in *acuens*, namely, 1·2 or 3·4. It has 1·2 because *V* segregates independently of the complexes in *maculans*·"N" (Emerson & Sturtevant, 1931). The 2 pairs which *maculans* gives with *acuens* are already provided for; hence *maculans* cannot have 11·12, 13·14.

$$\textit{maculans} = 1 \quad 2 \quad 5 \cdot 6 \quad 7 \cdot 10 \text{ or } 9 \cdot 8 \quad (\text{not } 11 \cdot 12 \quad 13 \cdot 14)$$

(xii) *Jugens* (a genom of *shulliana*, more commonly transmitted through the eggs)

<i>jugens</i> · <i>acuens</i>	=	⊙8, 3 pairs
<i>jugens</i> ^h <i>franciscana</i> E. + S.	=	⊙10, 2 pairs
<i>jugens</i> "N"	=	⊙10, 2 pairs
<i>jugens</i> <i>velans</i>	=	⊙12, 1 pair
<i>jugens</i> · <i>gaudens</i>	=	⊙14

Jugens gives 3 pairs with *acuens* and 2 pairs with ^h*franciscana* E. & S. It must therefore have an *acuens* chromosome not found in ^h*franciscana*, namely, 1·4 or 3·2 (not both). It gives 2 pairs with "N" and 1 pair with *velans*, and therefore has an "N" chromosome not found in *velans*, namely, 5·6 or 7·14 or 8·13. It cannot have 5·6, however, since it gives ⊙14 with *gaudens*. It must therefore have 7·14 or 8·13. Since it gives 2 pairs with ^h*franciscana* E & S and but 1 pair with *velans*, it must have 1 ^h*franciscana* chromosome not present in *velans*, namely, 5·6 or 7·10 or 9·8. Since it cannot have 5·6, it must have 7·10 or 9·8. But 7·10 and 7·14 are mutually exclusive, as are 9·8 and 8·13, if *jugens* has 7·10 it must therefore have 8·13, but if it has 9·8, it must have 7·14 (7·10 has been selected arbitrarily by Emerson + Sturtevant, 1931; we prefer to leave the matter open for the time being). No matter which of these pairs it has, it must have 11·12, for it gives 2 pairs with "N," and 8·13 in the one case and 7·14 in the other constitute one of these, 11·12 being the only other "N" chromosome which could be present in *jugens* (1·2 and 3·4 are excluded because *jugens* has 1·4 or 3·2, 5·6 is already excluded because *jugens* gives ⊙14 with *gaudens*).

$$jugens = 1 \cdot 4 \text{ or } 3 \cdot 2 \left\{ \begin{array}{cc} 7 \cdot 10 & 8 \cdot 13 \\ 9 \cdot 8 & 7 \cdot 14 \end{array} \right\} 11 \cdot 12$$

(xiii) *Albicans* (egg complex of *suaveolens* and *biennis*)

<i>albicans</i> · ^h <i>hookeri</i>	=	⊙14
<i>albicans</i> · <i>flavens</i>	=	⊙12, 1 pair *
<i>albicans</i> · ^h <i>Dalton</i>	=	⊙12, 1 pair
<i>albicans</i> ·"N"	=	⊙12, 1 pair
<i>albicans</i> · <i>velans</i>	=	⊙14
<i>albicans</i> · <i>gaudens</i>	=	⊙6, ⊙8

Albicans gives 014 with ^h*hookeri* and 012, 1 pair, with *flavens*. It therefore has 1·4 or 3·2 in common with *flavens*. On genetical grounds, it has been assigned 1·4 (Cleland + Blakeslee, 1931; Emerson + Sturtevant, 1931). It gives 1 pair with ^h*Dalton* and no pairs with ^h*hookeri*. It therefore has one ^h*Dalton* chromosome not present in ^h*hookeri*, i.e., 7·10 or 9·8. It gives 1 pair with “N” and no pairs with *velans*, and must therefore have one of the “N” chromosomes not in *velans*, namely, 5·6 or 7·14 or 8·13. It cannot have 5·6 because it gives no pairs with *gaudens*. It must have, therefore, 7·14 or 8·13. If it has 7·10, however, it cannot have 7·14 and must have 8·13; if it has 9·8, it cannot have 8·13 and must have 7·14. So *albicans* must have 7·10 8·13 or 7·14 9·8 (cp. Emerson + Sturtevant, 1931, p. 403, p. 405).

$$albicans = 1 \ 4 \ \begin{cases} 7 \ 10 \ 8 \cdot 13 \\ 7 \ 14 \ 9 \cdot 8 \end{cases}$$

(xiv) *Accelerans* (egg complex of *oakesiana*, from New England)

$$\begin{aligned} accelerans \cdot velans &= 014 \\ accelerans \cdot "N" &= 012, 1 \text{ pair} \\ accelerans \cdot ^hMateo &= 012, 1 \text{ pair} \\ accelerans \cdot flavens &= 06, 06, 1 \text{ pair} \end{aligned}$$

Accelerans gives 1 pair with “N,” and no pairs with *velans*. It therefore has 5·6 or 7·14 or 8·13, which are the only “N” chromosomes not found in *velans*. It gives 012 with ^h*Mateo* and must therefore have a ^h*Mateo* chromosome not present in *velans*, namely, one of 5·6, 7·10, 9·8. If it has 7·14 and not 5·6, it cannot have 7·10, and must have 9·8. If it has 8·13, and hence not 5·6, it must have 7·10. It may have, therefore, either 5·6 or 7·14 9·8 or 7·10 13·8. It gives 06, 06 with *flavens* and 014 with *velans*, and therefore has one *flavens* chromosome not present in *velans*. This is 1·4 or 3·2 or 5·6 or 7·8. The last is not possible, however, as *accelerans* must have 9·8 or 13·8 if it does not have 5·6. The possibilities for *accelerans* are therefore:

accelerans = 1 4 or 3·2 (with either 7·14 9·8 or 7·10 13·8);
or 5·6 (with others undetermined) (It cannot
have 1·2, 3·4, 5 8, 7·6, 9·10, 11·12, 13·14)

(xv) *Punctulans* (pollen complex of *chicaginesis*, from Illinois)

flavens·punctulans = ○8, 3 pairs
hookeri·punctulans = ○10, 2 pairs
albicans·punctulans = ○10, 2 pairs
acuens·punctulans = ○10, 2 pairs
rigens punctulans = ○14
excellens·punctulans = ○12, 1 pair

Punctulans (cp. Emerson + Sturtevant, 1931) gives 3 pairs with *flavens*, 2 pairs with *hookeri*, and therefore has 1 4 or 3·2. Since *pus* segregates in progeny of *albicans punctulans*, it has 1·4 (Renner). It gives 3 pairs with *flavens*, 2 pairs with *acuens*, and hence has 7 8 or 9·10. Since it gives ○14 with *rigens*, it does not have 9·10 and must have 7·8. It gives one pair with *excellens* and no pairs with *rigens*, it must therefore have an *excellens* chromosome not present in *rigens*, namely, one of 7·10, 9·8, 11·12, 13 14. Since it has 7·8 it cannot have the first two of these, and must have 11·12 or 13·14

punctulans has 1 4 7·8 11·12 or 13·14

(xvi) *Pubens* (egg complex of *nobska*, from New England)

pubens·β Iowa 6 = ○14
pubens·velans = ○14? (at least, no pair)
pubens·hookeri = ○12, 1 pair

Pubens gives ○14 with *β Iowa 6* and cannot therefore have 1·4 3·2. It gives no pairs with *velans* and one pair with *hookeri*. It therefore has a *hookeri* chromosome not in *velans*, i.e., 5·6 or 7·8 (cp. Emerson + Sturtevant, 1931, p. 407).

pubens = 5·6 or 7·8

(xvii) *Curvans* (pollen complex of *muricata*)

flavens·curvans = 06, 06, 1 pair (Renner)

hookeri·curvans = 06, 08

acuens·curvans = 04, 06, 2 pairs

Curvans gives one pair with *flavens* and no pairs with *hookeri*. It must therefore have a *flavens* chromosome not present in *hookeri*, namely, 1·4 or 3·2. Since *M* is segregated in the progeny of *flavens·curvans* (Renner), it has 3·2. It gives 2 pairs with *acuens*, one pair with *flavens*, hence must have an *acuens* chromosome not in *flavens*. This must be 7·10 or 9·8

curvans = 3·2 7·10 or 9·8

(xviii) *Flectens* (pollen complex of *cruciata*)

The pollen complex of Renner's strain of *cruciata*, derived apparently from material originating at Lake George, N. Y., differs by at least 1 segmental interchange from the pollen complex in our strain, obtained directly from the wild at Waterbury, Vermont. The following chromosome configurations have been obtained by Renner and involve his material.

flavens flectens = 04, 06, 2 pairs

rigens·flectens = 04, 08, 1 pair

velans·flectens = 06, 04, 04

Flectens (cp Renner, 1933) gives 2 pairs with *flavens*, one pair with *rigens*. It therefore has a *flavens* chromosome not found in *rigens*, i.e., one of 1·4, 3·2, 7·8, 11·12, 13·14. It gives no pair with *velans* so it cannot have 11·12 or 13·14. It gives 2 pairs with *flavens* and none with *velans*, so it has 2 *flavens* chromosomes not in *velans*, i.e., 2 of 1·4, 3·2, 5·6, 7·8. It has 1 pair with *rigens*, and so has a *rigens* chromosome not present in *velans*, or one of 5·6, 7·11, 12·13, 8·14. The genetic evidence indicates that in *rigens flectens* and *velans·flectens*, *P* and *R* are coupled, but separate from the rest of the complexes (Renner), hence that *flectens* has 1·4 and 3·2. It cannot therefore have 5·6 or 7·8. If it does not have 5·6, it must have 7·11 or 12·13 or 8·14.

flectens = 1·4 3·2 7·11 or 13·12 or 8·14.

The *flectens* from our material cannot have both 1·4 and 3·2, for it gives no pair with *argillicola* (○6, ○4, ○4), which has 1 4 or 3·2. We have not analyzed our material sufficiently as yet to say more about the segmental arrangement of its pollen complex

(xix) *argillicola* (genom of apparently homozygous *argillicola*, from Pennsylvania)

velans · *argillicola* = ○10, 2 pairs

acuens · *argillicola* = ○4, 5 pairs

rigens · *argillicola* = ○14

argillicola gives 2 pairs with *velans* and 5 pairs with *acuens*, so it must have 3 chromosomes in common with *acuens* which are not present in *velans* (3 of 1·4, 3·2, 5·6, 7·10, 9·8). Since it gives no pairs with *rigens*, it cannot have 5·6. If it has both 1·4 and 3·2, then it should give ○4 as part of its configuration with *velans*, which is not correct. So it cannot have both 1 4 and 3·2. With either 1 4 or 3 2 impossible, as well as 5·6, it must have both 7·10 and 9·8 to give 5 pairs with *acuens*. Neither 11·12 nor 13·14 can be involved in the ○ of 4 with *acuens*; if both were involved, *argillicola* would have all 3 of 1·4 3·2 5·6 common to *acuens*, which is impossible. If only one were involved, it would still have to have either 5 6 or both 1·4 and 3 2 common to *acuens*, both of which are impossibilities. Therefore *argillicola* has 11·12 13 14 in common with *acuens*. The ○ of 4 with *acuens* involves either 1 4 or 3 2, and 5·6 of *acuens*.

$$^{\text{argillicola}} = \begin{cases} 1 \cdot 4 \begin{Bmatrix} 3 \cdot 5 & 2 \cdot 6 \\ 3 & 6 & 5 \cdot 2 \end{Bmatrix} \\ 3 \cdot 2 \begin{Bmatrix} 1 & 5 & 4 \cdot 6 \\ 1 \cdot 6 & 5 & 4 \end{Bmatrix} \end{cases} \quad 7 \ 10 \ 9 \cdot 8 \ 11 \ 12 \ 13 \ 14$$

2. DISCUSSION AND CONCLUSIONS

(a) Studies in segmental arrangement have this year resulted in the assignment of full formulæ to 3 additional complexes. One of these (*acuens*, belonging to *grandiflora*, a form

from Alabama) has been reported upon elsewhere (Cleland 1935b). It has an arrangement of ends which places it definitely among the complexes of the California type. The other two are *rigens* (of *muricata*) and *fascians* (of *ostrea*). These complexes should prove to be very valuable as testers, since new chromosomes are involved in the interchanges producing them. In addition, the arrangements of several other complexes have been worked out almost completely. Thus, there remain but 2 alternatives for *decipiens*, and 4 alternatives for *blandina*, *elongans* and *stringens*. When completely worked out, these should also be valuable testers for further analyses of segmental arrangements.

(b) Two of the complexes in the table, α Iowa 6 and β Iowa 6, belong to a new race. This race turns out to be a complex-heterozygote, with balanced lethals and a circle of 14 chromosomes. Genetically, it is unusual in one respect, in that it forms 2 classes of pollen grains, but only one class of eggs. The reverse condition is common among Onagras, but this is the first instance in which this condition has been found (for description of Iowa 6 see appendix, p. 519).

(c) We may now consider the results of the year's study from the phylogenetic point of view, in order to discover whether they have any bearing upon the problem of inter-racial relationships. Of course, one cannot expect too much from a bare beginning, such as these studies represent. The complexes dealt with in this paper constitute but a small and scattering sample of the complexes actually existent in nature, and the data in respect to their segmental arrangements are for the most part still too meagre to afford a basis upon which to theorize with regard to relationships. Such indications of relationship as appear from this study, therefore, should be regarded of value mainly as suggestions to be followed up rather than as conclusions to be accepted.

The first indication of relationship resulting from the year's work comes from a study of *rigens* and *fascians*. It has become increasingly apparent that these two complexes have the same arrangement of segments, and that they are there-

fore in all probability closely related phylogenetically. This is suggested partly by the fact that the reasoning by which it has been possible partially to work out the segmental arrangement of *fascians* leads, so far as it goes, to a conclusion identical with that to which the reasoning in the case of *rigens* leads; it is suggested chiefly, however, by the fact that in every case in which *rigens* and *fascians* have both been studied in combination with a third complex (in 7 cases), they have given identical chromosome configurations. It seems quite probable, therefore, that they have the same arrangement of ends. This identity of segmental arrangement, in complexes which must have been separated geographically for well over a century, emphasizes the fact that segmental arrangements are quite stable, even in *Onagra*. Our whole experience indicates that the incidence of segmental interchange in this genus is high only in comparison with other genera, on the absolute scale, it is in reality very low. It would seem to be lower, in fact, in this case than the incidence of gene mutation, for in spite of identity of segmental arrangement, *fascians* and *rigens* are not entirely identical in their effect upon the phenotype. Thus among other minor differences *fascians* produces defective petals, and imparts a distinctive type of pink coloration to stem and pulvini of the leaves, including the base of the hypanthia, characters not produced by *rigens*.

Another suggestion of relationship has to do with *gaudens* and *rubens*. These two closely related complexes (with identical segmental arrangement) have hitherto failed to show any indication of close relationship to other complexes, except that Emerson and Sturtevant (1931) have pointed out that *gaudens* and *maculans* seem to give similar configurations with other complexes. We now find that *gaudens* and *rubens* show similarities in segmental arrangement with other complexes which suggest affinities in two different directions. On the one hand, they give O6 and 4 pairs with *rigens* and *fascians*, on the other hand, they give O4, O6 and 2 pairs with *maculans* (of *shulliana*) and *accelerans* (of *oakesiana*).

These configurations could represent differences of as few

as two interchanges in the case of O6 and 4 pairs, or three interchanges, in the case of O6, O4 and 2 pairs; and there is a possibility that their presence in these combinations is indicative of close phylogenetic relationship. However, *gaudens* or *rubens* produce quite dissimilar phenotypic effects from *rigens* or *fascians* or *accelerans* (there is more resemblance in the case of *maculans*), and consequently, one should be cautious about pushing the possibility of relationship, until the reactions of all these complexes are better known with other complexes. Should it appear later that *rigens* and *fascians* are in reality rather closely related to *gaudens* and *rubens*, they would constitute a connecting link between *gaudens* and *rubens* on the one hand and the California type of complex on the other, for *rigens* and *fascians* give O6 with *hookeri* de Vries.

One of the complexes most noteworthy for its failure to show relationship in segmental arrangement with other complexes is *albicans*. Until recently, it has shown no similarity to other complexes. However, Renner has recently found that it gives O6 and 4 pairs with *flectens*, and there is a slight possibility that it is related in segmental arrangement with *jugens*, of *shulliana*. These two have not been crossed as yet, but they show very similar chromosome configurations when crossed with other complexes. Since the configurations found in these hybrids, however, include in all cases large circles, weight is not necessarily to be attached to this similarity. For instance, the presence of 11·12 in *jugens* and its absence in *albicans* would be sufficient to account for the difference in most of the cases. However, the similarity in phenotypic effect of *jugens* and *albicans* suggests the advisability of bearing in mind a possible relationship between them.

The next case of possible phylogenetic relationship is that of *Iowa 6*. From the standpoint of segmental arrangement, this race shows on the one hand a relationship to *cockerelli* (as was to be expected from the phenotypic resemblance of the two races), and on the other hand a possible relationship to *shulliana*. Its pollen complex, β *Iowa 6*, is apparently very similar to *elongans*, the pollen complex of *cockerelli*. These

complexes have not been brought into combination as yet, inasmuch as both are pollen complexes. However, their segmental arrangements, so far as these have been worked out comparatively, are the same; and, in addition, the five cases in which both complexes are known in combination with a third complex have shown either identical chromosome configurations (3 Os 4 with *franciscana* $E + S$, 2 Os 4 with *acuens*, 04, 08 with *hookeri*) or configurations which might be interpreted as showing a difference between the complexes of but a single interchange (*truncans*- β Iowa 6, 04, 08 vs. *truncans*-*elongans* 012, *velans*- β Iowa 6, 04, 08 vs. *velans* *elongans* 04, 06). These cases of similarity or identity in chromosome configuration are probably of phylogenetic significance, inasmuch as they involve for the most part, small circles, and it has been pointed out previously (Cleland 1935a) that there is very little likelihood of the appearance of configurations composed of small circles unless the complexes forming these configurations have had a relatively recent common origin.

While β Iowa 6 is apparently related in segmental arrangement to *elongans*, α Iowa 6 shows a resemblance to *maculans* of *shulliana*, for it gives 04, 04, 3 pairs with it, and may therefore differ from it by as few as 2 segmental interchanges. Furthermore, it is interesting to note that although α and β Iowa 6 are so unrelated to each other in segmental arrangement that they give 014 when combined, both nevertheless show relationship to the California group of complexes. β Iowa 6 gives 04, 04, 04, 1 pair with *Devil's Gate*, 04, 04, 3 pairs with *acuens*, and 04, 08 with *hookeri* and *velans*. These configurations would seem to indicate rather close relationship in segmental arrangement between the complexes involved (β Iowa 6 showing a minimum possible difference of 2 interchanges from *acuens*, of 3 interchanges from *Devil's Gate*, of 4 interchanges from *velans* and *hookeri*). On the other hand, α Iowa 6 gives 04, 06, 2 pairs with *Devil's Gate* which suggests a possible minimum difference of but 3 interchanges. The probabilities are that the two complexes of

Iowa 6 are each related not too distantly to the California alliance, but along somewhat different lines

The last form to be mentioned from the standpoint of its phylogenetic relationship is *argillicola*. This interesting race is found in the mountains of West Virginia and central Pennsylvania and is probably to be regarded as a relict species. The strain which has been studied is from Huntingdon, Pennsylvania, and was sent to the first author by Dr Edgar T. Wherry. *Argillicola* is exceptional among *Onagras* in the north-eastern United States, so far as these are known, in having large flowers, long styles, entirely paired chromosomes, high fertility and in being apparently alethal and homozygous.¹ Coupled, however, with these features, which are characteristic of the California forms, rather than those from the east, we find *argillicola* displaying many of the phenotypic characters which are produced by the pollen complexes of the *muricatas*, such as sub-terminal sepal tips, narrow foliage, bent stem tips, etc. In particular, *argillicola* resembles *flectens* of *cruciata* very closely in its phenotypic effect upon habit and foliage characters. In view of this composite phenotypic effect, therefore, it is interesting to determine whether *argillicola* bears a close resemblance in segmental arrangement to *flectens* or to the California complexes, or whether it shows no relationship to either.

A few *argillicola* crosses have now been studied, and these indicate an approach in segmental arrangement to the California alliance, and a probably somewhat more distant relationship to *flectens* and the pollen complexes of the *muricata* alliance in general. The complex closest to *argillicola* in segmental arrangement is *acuens*, from Alabama, which differs from it by but a single interchange (O4, 5 pairs), *acuens*, in turn, differs from the commonest arrangement found in California by but a single interchange, so that *argillicola* is possibly but 2 interchanges removed from the commonest

¹ A strain of *argillicola* from White Sulphur Springs, W. Va., which has just been reported upon by Mickan, a student of Renner, is apparently an isogamous-heterozygous form, with balanced lethals and with O4 and 5 pairs. The genetic differences between its complexes, however, are minor in character.

California arrangement¹ Among the pollen complexes of the *muricata* alliance, *^hargillicola* is known so far with *denudans* of *oakesiana*, β *ostrea* of *ostrea* and *flectens* of *cruciata*. It shows an indication of a closer affinity with β *ostrea* than with the others, producing $\odot 4$, $\odot 6$ and 2 pairs with it. With *denudans*, it gives $\odot 4$, $\odot 10$, and with *flectens* $\odot 6$, $\odot 4$, $\odot 4$. The difference between *^hargillicola* and β *ostrea* represents a possible minimum of 3 interchanges, that with *flectens* a possible minimum of 4. The possibility that *argillicola* is a relict form suggests that complexes of the California type may possibly have been indigenous in the east for a long time. The fact that its genom is so close to *acuens* in segmental arrangement, suggests that a phylogenetic connection may exist between *argillicola* and the *grandiflora* assemblage of Alabama. A number of forms from regions intermediate between West Virginia and Alabama are being grown at present and may throw some light upon this relationship. It is possible, furthermore, that *argillicola* is a transitional form which points to the origin of complexes of the *flectens* type, possibly from those of the California type. These possibilities will be borne in mind as further work is done on the eastern forms.

From this discussion, it will be seen that definitive conclusions as to the phylogenetic affinities of forms indigenous to regions east of the Rockies cannot as yet be made, but the bare beginning of work on these forms does suggest certain possibilities to be followed up as data become more extensive. At least it becomes clear from the discussion what the nature of the evidence is, and the sort of conclusion which may be drawn as our basis of fact grows. Among other problems, it may in time be possible to determine the origins of various of the genetic races which have played so prominent a role in *Oenothera* research. Thus, the evidence, though meagre, suggests that *lamarckiana* may be the product of the union of a

¹ One of the complexes in Micken's material has the same segmental arrangement as *flavens*. The other differs from *flavens* segmentally by a single interchange ($\odot 4$, 5 pairs), and from *^hhookeri* by 2 interchanges ($\odot 4$, $\odot 4$, 3 pairs). In this material, also, therefore, the complexes are of the California type from the standpoint of segmental arrangement.

complex of western affinity (*velans*) and one of eastern affinity (*gaudens*), for *velans* is a complex of the California type, and *gaudens* shows some possibility of relationship to *maculans* from New Jersey and *fascians* from New England. Similarly, *suaveolens* is composed of *albicans*, whose closest affinities so far would seem to lie in the direction of *jugens* from New Jersey and *flectens* from New England, and *flavens*, which is definitely of the *acuens-hookeri* type. *Biennis* on the other hand is composed of the complexes *albicans* and *rubens* (the latter very close to *gaudens*), both of which may be of eastern affinity.

Summary.—1. Considerable advance has been made in the analysis of the segmental arrangements of a number of complexes, belonging to certain races from the eastern or central western portions of the United States. The reasoning upon which these analyses are based has been presented in full. The arrangements of 3 complexes have been completely determined. These complexes are of value as testers in the further work of analyzing segmental arrangements.

2. From this work certain relationships between complexes are suggested, relationships in some cases involving complexes which had hitherto shown little in the way of affinities.

3. Clues as to the possible origins of some of the chief genetic races of *Onagra* are furnished.

4. In the appendix will be found descriptions of *argillicola* and "Iowa 6," together with brief characterizations of a large number of hybrids involving the complexes discussed in this paper. Complexes of "Iowa 6" are compared as to their phenotypic effect (p. 520).

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BRIEF DESCRIPTION OF SPECIES AND HYBRIDS

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1. *Argillicola* and its Hybrids*Æ argillicola*

Seed contributed by Dr Edgar T Wherry It was collected at the Morris Arboretum, University of Pennsylvania, in the fall of 1933, from rosettes brought in the preceding April from Huntingdon, Pennsylvania These plants were open pollinated, but were grown far from any other *Oenotheras*.

The race has a strong biennial tendency, but matured in 1934 in one season The 1935 culture did not flower until 1936

Description —Much branched from dense rosette, the branches sprawling in disorderly fashion, semi-procumbent, the stem tips strongly nodding, central shoots, when present, semi-procumbent

Leaves very narrow (a typical rosette leaf 23×1.5 cm), often

wavy, rather trough-shaped, mostly standing erect on stems, very dark green, essentially glabrous, with red midribs, marginal teeth short, widely separated, marginal glands often reddened

Stems bright red below, green above, with very few long, semi-appressed hairs and a few short felty hairs, tips nodding, red papillæ doubtfully discernible *Bracts* erect, flaring widely at the tip, light green *Buds* slender, green, except for reddened calyx margins, thin-skinned, long and tapering (cone 3 cm, hypanthium 4 cm, ovary 1 cm), with long, delicate spreading, subterminal sepal tips, occasionally red-tipped, pubescence almost absent, a few short glandular hairs and a few long, spreading ones being present *Style* long, petals broader than long (e.g., 2.2 mm long \times 2.6 mm broad), flowers ca 7–8 cm across, open-pollinated *Fruits* narrow, long, tapering, standing out stiffly from the stems and bending upward, often at a distance from the stem, becoming more or less reddened

This is a most striking plant. In flower size it resembles the *hookeri* alliance. In foliage characters, however, and in the possession of nodding stems and spreading sepal tips, it shows affinities with the pollen complexes of the *muricata* alliance. It is in particular so close to *flectens*, the pollen complex of *cruciata*, in phenotypic effect, that corresponding hybrids of the two are scarcely to be distinguished. Plants so far have been entirely uniform in appearance. They are very similar in phenotypic appearance to the *argillicola* studied by Micken (1936), from White Sulphur Springs, West Virginia.

Chromosome Configuration—Two plants of the first generation were examined and both had 7 pairs.

Pollen Count (2 pls)—Good 400, empty 6 (= 1.5 per cent), total 406

1935 118 $\text{\textcircled{E}}$ (*argillicola* \times *cruciata*) (1934 80, pl 2 \times 1934 81, pl 2)

But 5 seeds were set, all germinated and 5 plants were transferred to field (*argillicola* β *cruciata* = *flectens* ?)

Parent races are similar in habit, which habit was shared by hybrids, stems sprawling, numerous, central shoots absent, plants but 40 cm high (although in good soil). Rosette leaves very numerous. Plants very much like *argillicola*, but with green midribs, more widely flaring bracts, small flowers and narrow, though usually perfect, petals. Foliage narrow, lower leaves dark green, upper ones light green, margins reddened, stems reddened at base, without red papillæ, buds slender, green, with long hypanthia and subterminal sepal tips. Style short, flowers self-pollinating. Petals

PLATE I

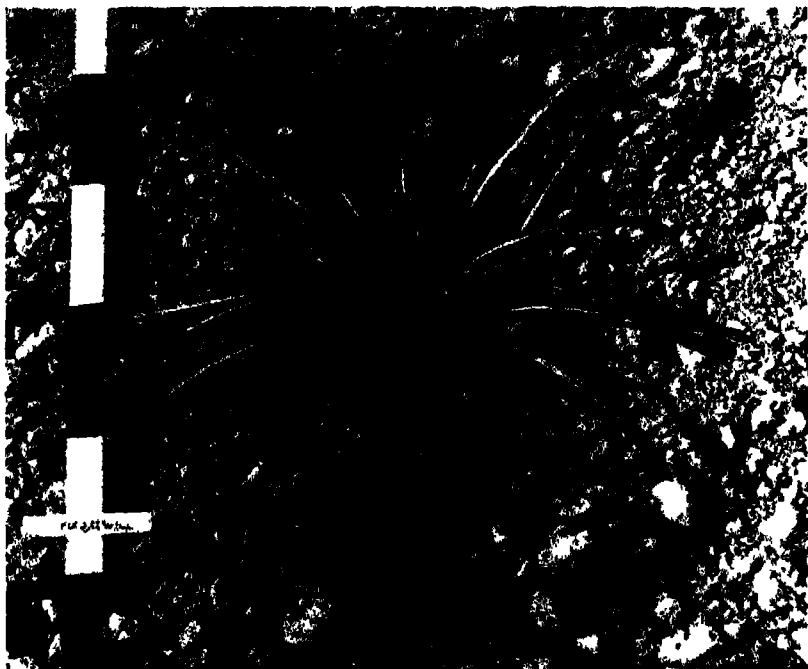


FIG 1 *Enothera argillicola*, mature rosette



FIG 2 *Enothera argillicola*

not cruciate, only occasionally defective, but usually narrow
Fruits typical of *argillicola* Pubescence, both long and short,
 almost absent

Chromosome Configuration (1 pl) — 04, 04, 06

Pollen Count (1 pl) — Good 94, "inactive" 7, empty 89 (= 46.8 per cent), total 190

1935 113 *CE* (*argillicola* × *r-lamarckiana*) (1934 80, pl 12 × 1934 1, pl 7)

Seeds germinated, 15 (45.5 per cent), ungerminated, 18 (4 with, 14 without embryo) total 33 Transferred to field, 4 plants (*argillicola gaudens*)

All plants were *latea*, the reciprocal cross yielded only *velutinae*
 Plants low (30 cm.), the stems all lateral, almost procumbent
 Leaves were intermediate between parents in width, were dark green, somewhat red-flecked when young, much crinkled, almost glabrous, with green midribs and brownish marginal glands *Stems* reddened at base and bent at tips as in *argillicola*, pubescence sparse
 Bracts nearly erect, as in both parents Buds large, slender, tapering, wholly green, nearly glabrous, sepal teeth bowed, not subterminal Style long and flowers large (5.5–6 cm.), as in both parents *Fruits* tapering as in *argillicola*, but short, as is usual in *gaudens* hybrids On the whole, plants showed *gaudens* and *argillicola* influences about equally strongly

Chromosome Configuration (1 pl) — 014

Pollen Count (1 pl) — Good 200, "inactive" 2, empty 225 (= 52.7 per cent), total 427

1935 107 *CE* (*argillicola* × *oakesiana*) (1934 80, pl. 2 × 1934. 21, pl 8)

But 6 seeds were set, all germinated, but only 2 survived, of which one bloomed (*argillicola denudans*) Plant 20 cm high, with a single, almost procumbent, much-branched rosette branch, showing thus the *argillicola* type of habit Plant also resembled *argillicola* in having slight red color in midribs, red marginal glands, stems reddened below, a few long hairs on stems, buds and fruits, slender tapering fruits, often standing at a wide angle to stem It showed the *denudans* influence in the flaring of bracts, shortening of style so that flowers were self-pollinating Both parents contributed nodding stem tips, dark green narrow foliage, green buds, subterminal sepal tips Flowers were rather small in size (3.5–4 cm.), petals broader than long, with shallow sinus without tooth, glandular pubescence practically absent

Chromosome Configuration.—The only plant which bloomed showed $\bigcirc 4$, $\bigcirc 10$.

Pollen Count (1 pl) —Good 200, "inactive" 3, empty 281 (58 per cent), total 484

1935: 112 CE (*argillicola* \times *ostrea*) (1934. 80, pl. 12 \times 1934. 23, pl 5)

Seeds germinated, 51 (69 per cent); ungerminated, 23 (8 with, 15 without embryo). total 74 Transferred to field, 7 plants (*^hargillicola* β *ostrea*)

Plants with habit of *argillicola*, stems procumbent or nearly so, rising but 20–30 cm from soil. They resembled *argillicola* also in slight traces of color in midribs and at base of stem, and in fruit shape and position. *β ostrea* influence was seen in the flaring bracts, the frequently defective or even cruciate petals, occasional splotches of red color on foliage, and shortened style. Both parents contributed narrow, dark green leaves, bent stem tips, slender, green buds, subterminal sepal tips, sparse spreading pubescence Flowers were ca. 3 cm across. Marginal teeth of leaves were scarcely colored Red papillæ absent

Chromosome Configuration (3 pls) — $\bigcirc 4$, $\bigcirc 6$, 2 pairs

Pollen Count (1 pl) —Good 200, "inactive" 1, empty 306 (60.4 per cent), total 507.

1935 128 CE (*grandiflora* \times *argillicola*) (1934. 2, pl. 9 \times 1934 80, pl 12)

Seed germination not recorded: 29 seedlings, mostly chlorotic, 6 plants transferred to field

Plants chlorotic when seedlings, many dying in seed pan, 6 plants survived, becoming green (2 *acuens* *^hargillicola*, 4 *truncans* *^hargillicola*)

Acuta were intermediate in habit, showing conflict between bushy habit of *acuens* and straggling habit of *argillicola* Characters dependent upon *^hargillicola* a sparsity of long spreading pubescence; bent stem tips, subterminal sepal tips, curved tapering fruits *Acuens* apparently suppressed midrib color Characters received from both parents. red basal stem color (chiefly from *^hargillicola*), green stem tips, near-absence of felty pubescence, narrow foliage (intermediate), erect bracts, large flowers, green, slender buds, long styles.

Truncata were similar in habit to *acuta* They differed from the latter in the following ways. (characters due to *truncans*) presence of felty pubescence on stem and buds, and flaring bracts; (characters

due to both *argillicola* and *truncans*) brighter red basal stem color, red midribs.

Chromosome Configurations *truncata* (3 pls.) — $\bigcirc 12$, 1 pair
acuta (2 pls.) — $\bigcirc 4$, 5 pairs.

Pollen Counts. *acuta* (1 pl) — Good 200, "inactive" 1, empty 33 (14.1 per cent), total 234

1935: 159 Σ . (*r-lamarckiana* \times *argillicola*) (1934: 1, pl. 7 \times 1934: 80, pl. 12)

Seeds germinated, 58 (66 per cent), ungerminated, 30 (17 with, 13 without embryo). total 88. Transferred to field, 23 plants (*velans* *argillicola*).

Plants chlorotic as seedlings, recovering to a good green, often with chlorotic patches. Central shoots absent, branches widely spreading, not procumbent, plants 50 cm high. *Argillicola* characters were: red midribs, somewhat pigmented leaf margins; almost entire absence of felt, and sparsity of longer pubescence; bent stem tips, tapering, curved fruits. Characters attributable to *velans*: waviness of leaves, red stem tips, red papillæ, bracts, bud cones and hypanthia reddened, sepal tips not subterminal, fruit stout. Plants were intermediate in leaf breadth, and received from both parents red basal stem color, upright bract position, large flowers and long styles.

Chromosome Configuration (3 pls.) — $\bigcirc 10$, 2 pairs

Pollen Count (1 pl.) — Good 200, "inactive" 3, empty 161 (44.2 per cent), total 364.

1935: 165 Σ . (*muricata* \times *argillicola*) (1934: 3, pl. 9 \times 1934: 80, pl. 12)

Capsules mostly sterile, only 2 seeds obtained. These germinated; one plant bloomed, the other remained a rosette (*rigens* *argillicola*).

Rigens characters: central shoot, red papillæ, faint trace of color under bracts and on base of bud cones, appressed pubescence on buds, short style, sepal tips not subterminal (though spreading, due to *argillicola*). *Argillicola* characters: leaves with red glandular teeth, some red in midribs, stems tending to sprawl, even the central shoot, pubescence reduced in amount, stem tips bent, sepal tips spreading (though not subterminal), fruits tapering, curved. Plants intermediate in flower size, both complexes helped to produce narrow leaves, erect bracts.

Chromosome Configuration (1 pl.) — $\bigcirc 14$

Pollen Count (1 pl.) — Good 200, "inactive" 92, empty 489 (62.6 per cent), total 781.

2 *Hybrids of blandina*

1933. 26 *CE* (*blandina* × *grandiflora*) (1932: 24, pl. 13 × 1932: 27, pl. 15)

Seeds germinated, 99 (99 per cent), ungerminated, with embryo, 1 total 100. Transferred to field, 30 plants (11 [^]*blandina acuens*, 19 [^]*blandina truncans*).

[^]*Blandina* gave to all plants red papillæ, purple stem tips, red striped bud cones. The distinctions between *acutæ* and *truncatæ*, well-known from other crosses, were in this case particularly clear. In habit, plants were typical *grandiflora* hybrids, being tall and bushy (*acutæ* 115 cm, *truncatæ* 130 cm.)

Chromosome Configurations *acutæ* (3 pls) — O4, O4, 3 pairs.
truncatæ (3 pls) — O12, 1 pair.

Pollen Counts. *acutæ* (1 pl) — Good 475, empty 33 (6.5 per cent), total 508

truncatæ (1 pl) — Good 416, empty 596 (58.9 per cent), total 1012

1933. 1 *CE* (*blandina* × *hookeri*) (1929. 7, pl. 7 × 1929. 14, pl. 5)

Seeds germinated, 27 (77 per cent), ungerminated, without embryo, 8 total, 35. Transferred to field, 15 plants ([^]*blandina* · [^]*hookeri*).

Plants were pale and sickly as seedlings, but slowly recovered and became in the field a good green, they showed a weak tendency toward central shoot production. In most respects, [^]*blandina* and [^]*hookeri* produce similar phenotypes and hence plants were very much like robust *hookeri* plants.

Chromosome Configuration.—Renner (1933) has reported O6 and 4 pairs for this combination.

Pollen Count (1 pl) — Good 400, "inactive" 2, empty 98 (19.6 per cent), total 500

1933: 25 *CE* (*blandina* × "*Mateo*") (1932. 24, pl. 13 × 1932. 34, pl. 2)

Seeds germinated, 93 (93 per cent), ungerminated, 7 (with embryo 2, without 5): total 100. Transferred to field, 15 plants ([^]*blandina* [^]*Mateo*).

Plants lacked central shoots, rosette branches widespread. Characteristics of *Mateo* were on the whole accentuated by [^]*blandina*, so that pigmentation was heavy in stems (basal and tips), papillæ, bracts and buds. Leaves were moderately broad, with frequent trace of pink in midribs. Stems and buds were densely hairy, the

long hairs erect Two classes were present with respect to height and bushiness, as is true generally in *Mateo* hybrids (6 tall, 6 dwarf, 3 remained rosettes). The tall plants averaged 75 cm, the dwarfs 50 cm

Chromosome Configurations were not determined, since this combination should have the same configuration as *chicaginesis* \times *blandina* (which see)

Pollen Count (1 pl) — Good 400, empty 31 (7.2 per cent), total 431

1933 2 Σ (*blandina* \times *muricata*) (1929. 7, pl 2 \times 1929. 3, pl 5)

Seeds germinated, 93 (93 per cent), ungerminated, 7 (4 with embryo, 3 without) total 100

Seedlings were yellowish and died early Evidently, *blandina* plastids are unable to function in the presence of the combined ^h*blandina* and *curvans* gene complexes

1933 3 Σ (*blandina* \times *suaveolens*) (1929 7, pl 7 \times 1929 11, pl 10)

Seeds germinated, 46 (46 per cent), ungerminated, 54 (20 with embryo, 34 without) total 100 It is probable that the age of the seeds was responsible for reduced germination. Transferred to field, 15 plants (^h*blandina flavens*)

Plants typical *flavæ*, but with strong pigmentation of stems, bracts and buds, red papillæ, and abundant spreading pubescence Central shoots present, rosette branches widely spreading, plants 85 cm high

Chromosome Configuration (3 pls) — $\bigcirc 6$, $\bigcirc 4$, 2 pairs

Pollen Count (1 pl). — Good 400, "inactive" 8, empty 82 (16.7 per cent), total 490

1933 28 Σ . (*chicaginesis* \times *blandina*) (1932. 28, pl 1 \times 1932: 24, pl. 13)

Seeds germinated, 96 (96 per cent); ungerminated, 4 (1 with, 3 without embryo) total 100 Transferred to field, 15 plants (*excellens* ^h*blandina*).

Central shoots present, rosette branches widely spreading, plants 1 m. high. The influence of ^h*blandina* was seen in slight stem tip coloration, red papillæ, red color on bracts and bud-cones. Foliage was intermediate in leaf breadth, showing in other respects rather typical *excellens* characters.

Chromosome Configuration (3 pls) — $\bigcirc 4$, 5 pairs

Pollen Count (1 pl) — Good 241, "inactive" 4, empty 502 (67.2 per cent), total 747

1933: 30 *CE* (*franciscana* de *V.* \times *blandina*) (1932: 84, pl. 2 \times 1932: 24, pl. 13)

Seeds germinated, 91 (91 per cent); ungerminated, 9 (1 with, 8 without embryo). total 100 Transferred to field, 15 plants.

Central shoots absent, rosette branches almost prostrate, plants low. Leaves intermediate in breadth, wavy-crinkled, with white midribs and purple margins. In most other characters, the 2 parents are rather similar. Felty pubescence on stems and glandular pubescence on buds heavier than in *franciscana* and sepal tips a bit thicker, otherwise, buds like *franciscana*.

Chromosome Configuration (2 pls.) — $\bigcirc 6$, 4 pairs

Pollen Count (1 pl.) — Good 400, empty 97 (19.5 per cent), total 497

1933 33 *CE* (*r-lamarckiana* \times *blandina*) (1932: 60, pl. 15 \times 1932: 24, pl. 13)

Seeds germinated, 99 (99 per cent); ungerminated, with embryo, 1 total 100. Transferred to field, 29 plants (8 *gaudens* \times *blandina*, 21 *velans* \times *blandina*). These combinations have been studied phenotypically by de Vries (1917, 1918), and need not be re-described.

Chromosome Configurations. *lata* (3 pls.) — $\bigcirc 10$, 2 pairs.

velutina (3 pls.) — $\bigcirc 8$, 3 pairs

Pollen Counts. *lata* (1 pl.) — Good 400, "inactive" 7, empty 170 (29.4 per cent), total 577.

velutina (1 pl.) — Good 400, "inactive" 0, empty 78 (16.3 per cent), total 478.

1933. 9 *CE* (*muricata* \times *blandina*) (1929: 3, pl. 5 \times 1929: 7, pl. 2)

Seeds germinated, 55 (55 per cent), ungerminated, 45 (5 with, 40 without embryo) total 100 Transferred to field, 15 plants (*rigens* \times *blandina*)

Plants were uniform, 125 cm. high, with poorly developed central shoots except in 2 plants. They resembled (*muricata* \times *r-lamarckiana*) *rigens velans* in most respects, differing chiefly in having a slightly greyer caste, and shorter fruits.

Chromosome Configuration (3 pls.) — $\bigcirc 8$, 3 pairs

Pollen Count (1 pl.) — Good 84, "inactive" 74, empty 286 (64.4 per cent), total 444.

3. *Hybrids of erythrina*

1933: 6 *OE*. (*erythrina* × *r-lamarckiana*) (1929: 13, pl. 12 × 1929: 1, pl. 3)

Seeds germinated, 50 (50 per cent), ungerminated, 50 (20 with, 30 without embryos). total 100. Transferred to field, 26 plants (all *velutina*).

Erythrina is by composition *velans* ^{*h*}*decipiens*. Since all these plants received the lethal-bearing *velans* from the *lamarckiana* parent, it is certain that they must have received ^{*h*}*decipiens* from *erythrina*.

Plants 120 cm high, mostly with central shoots, which in a majority were no higher than the erect rosette branches. This complex-combination has been described by de Vries (1919). Pigmentation characters were greatly accentuated.

Chromosome Configuration (2 pls) — $\bigcirc 6$, 4 pairs

1933: 8 *OE* (*erythrina* × *suaveolens*) (1929 13, pl. 12 × 1929 11, pl. 10)

Seeds germinated, 98 (98 per cent), ungerminated, 2 (1 with, 1 without embryo): total 100. Transferred to field, 18 plants.

All plants but one were clearly *velans flavens*. The single plant of ^{*h*}*decipiens flavens* differed from the others in having broader leaves, less cone color, fewer long hairs on buds, longer style, more delicate and longer sepal tips, fruits red striped and shorter.

Chromosome Configurations *velans flavens* (3 pls) — $\bigcirc 4$, $\bigcirc 4$, 3 pairs

^{*h*}*decipiens flavens* (1 pl) — $\bigcirc 4$, $\bigcirc 4$, 3 pairs

Pollen Count *velans flavens* (1 pl.) — Good 200, "inactive" 55, empty 705 (73.4 per cent), total 960

1933: 5 *OE* (*hookeri* × *erythrina*) (1929. 14, pl. 6 × 1929: 13, pl. 13)

Seeds germinated, 96 (96 per cent), ungerminated, 4 (1 with, 3 without embryo). total 100. Transferred to field, 29 plants. Two classes were to be expected, ^{*h*}*hookeri*·^{*h*}*decipiens* and ^{*h*}*hookeri velans*.

Plants were uniform and apparently all ^{*h*}*hookeri* ^{*h*}*decipiens*. They differed from ^{*h*}*hookeri velans* in having broader leaves, buds more scarlet and less purple-red, longer and more delicate sepal tips, deeper yellow petals, and stouter, redder fruits.

Chromosome Configuration (7 pls.) — $\bigcirc 4$, 5 pairs.

Pollen Count (1 pl.) — Good 400, "inactive" 3, empty 139 (25.6 per cent), total 542.

1933 4 $\text{\textcircled{E}}$ (*r-lamarckiana* \times *erythrina*) (1929. 1, pl. 3 \times 1929: 13, pl 12)

Seeds germinated, 73 (73 per cent), ungerminated, 27 (18 with, 9 without embryo). total 100. Transferred to field, 30 plants.

Three combinations were possible. *gaudens* ^{*h*}*decipiens*, *gaudens velans* and *velans* ^{*h*}*decipiens*. There were 2 plants of *gaudens* ^{*h*}*decipiens* and the rest were *velans* ^{*h*}*decipiens*. No *gaudens* ^{*h*}*velans* were present. *Velans* ^{*h*}*decipiens* plants resembled their reciprocal in every respect. The *gaudens* ^{*h*}*decipiens* differed from *gaudens velans* (= *lamarckiana*) principally in having lighter, yellower leaves which were not quite as broad, greener buds, scantier spreading pubescence, petals deeper yellow.

Chromosome Configurations—*velans* ^{*h*}*decipiens* (3 pls) — $\text{\textcircled{O}}$ 6, 4 pairs
gaudens ^{*h*}*decipiens* (1 pl) — $\text{\textcircled{O}}$ 10, 2 pairs.

Pollen Counts. *velutina* (1 pl) —Good 400, "inactive" 3, empty 21 (4.95 per cent), total 424
lata (1 pl) —Good 400, "inactive" 13, empty 238 (36.5 per cent), total 651.

1934. 127 $\text{\textcircled{E}}$ (*muricata* \times *erythrina*) (1929. 3, pl 10 \times 1929: 13, pl 13)

Seeds germinated, 5 (4.1 per cent), ungerminated, 116 (96 with, 20 without embryo). total 121. Only 1 plant survived to maturity (*rigens* ^{*h*}*decipiens*). Poor germination no doubt due to age of seed.

Plant 135 cm tall, with prominent central shoot, and erect rosette branches, ^{*h*}*decipiens* modified the effect of *rigens* in enlarging hair bases, in giving strong color to stem tips, and fairly noticeable color to bud cones, and in lengthening sepal tips. Fruits were red-striped, as in *erythrina*. In other characters the influence of *rigens* predominated.

Chromosome Configuration (1 pl) — $\text{\textcircled{O}}$ 6, 4 pairs

Pollen Count (1 pl) —Good 200 "inactive" 112, empty 366 (54 per cent), total 678.

4. Hybrids of *cockerelli*

1932: 41 $\text{\textcircled{E}}$ (*cockerelli* \times *chicaginensis*) (1930: 7, pl. 1 \times 1930: 18, pl. 1)

Seeds germinated 84 (84 per cent), ungerminated, 16 (10 with, 6 without embryo). total 100. Transferred to field, 15 plants (*curtians punctulans*)

Plants uniform, 1 m. high, with central shoots. The phenotypic effects of the 2 complexes are very similar, both contributing rather narrow, grey-green leaves, free of pigment, stems slightly purpled at tip, green below, red papillae, rather stout, wholly green buds, appressed pubescence on buds.

Chromosome Configuration (3 pls) — $\bigcirc 10$, 2 pairs

1932: 40 \mathcal{E} (*cockerelli* \times *grandiflora*) (1930. 7, pl. 1 \times 1930. 16, pl. 2)

Seeds germinated, 93 (93 per cent), ungerminated, 7 (2 with, 5 without embryos), total 100. Transferred to field, 30 plants (13 *curtians-acuens*, 17 *curtians truncans*).

acutæ Plants somewhat chlorotic, all but 3 dying before flowering. Central shoots present, *curtians* produced stems reddened at the tip, with red papillæ, leaves moderately broad, pubescence of buds increased in amount, and semi-appressed. The complexes cooperated in producing white midribs, weak basal stem color, green buds and bracts.

truncatæ Plants tall, bushy, with central shoots, in most respects showing the predominating influence of *truncans*. *Curtians* modified the *truncans* effect chiefly in producing red papillæ, red stem tips, increased pubescence on buds.

Chromosome Configurations acutæ — Two plants were examined, one of which had $\bigcirc 12$, which is probably the correct configuration, the other had $\bigcirc 4$, $\bigcirc 4$, 3 pairs, which is the configuration of *elongans acuens*, so that this plant was probably a metachline. It was not recognized as such in the field. *truncatæ* Two plants showed $\bigcirc 14$ as their configuration.

1932 44 \mathcal{E} (*cockerelli* \times "*Johansen*") (1930 7, pl. 11 \times 1930 10, pl. 2)

Seeds germinated, 82 (82 per cent), ungerminated, 18 (4 with, 14 without embryo), total 100. Transferred to field, 15 plants (*curtians* \times *Johansen*).

Plants showed considerable resemblance to "*Johansen*," but had cone and bract color reduced, pubescence on buds somewhat appressed, flowers somewhat reduced in size.

Chromosome Configuration (3 pls) — $\bigcirc 4$, $\bigcirc 6$, 2 pairs

1932: 42 \mathcal{E} . (*cockerelli* \times *r-lamarckiana*) (1930. 7, pl. 1 \times 1930. 2, pl. 1)

Only 8 seeds were set, all of which germinated. All plants were transferred to field; all were *curtians-gaudens*. This hybrid has been

made previously by de Vries (Grup. Artbild; p. 117), and Oehlkers (1921, p. 6) Plants were typical *latea*, except that they had red papillæ, red stem tips, rather heavy pubescence and quite small flowers.

Chromosome Configuration (3 pls.).—O14

1932: 47 *E* (*chicaginensis* × *cockerelli*) (1930: 18, pl 1 × 1930: 7, pl 1)

Seeds germinated, 95 (95 per cent); ungerminated, 5 (2 with, 3 without embryo): total 100 Transferred to field, 15 plants (*excellens elongans*).

According to de Vries (Grup Artbild, p 75), these hybrids resemble closely the maternal parent. This is correct, *elongans* influencing the phenotype only in minor and ill-defined ways. Plants were robust, bushy, most stems becoming in time fasciated.

Chromosome Configuration (1 pl.)—O4, O4, O4, 1 pair

1931. 19 *E*. (*grandiflora* × *cockerelli*) (1930: 16, pl. 2 × 1930: 7, pl. 1)

Seeds germinated, 63 (79 per cent); ungerminated, 17 (7 with, 10 without embryo): total 80 Transferred to field, 30 plants (13 *acuens elongans*, 14 *truncans elongans*, 2 aberrants, 1 died)

Plants were typical *acutæ* and *truncatæ*. The usual differences between *acuens* and *truncans* combinations were clearly observed influence of *elongans* was scarcely to be noticed in the phenotype, except in the shortened style.

Chromosome Configurations. *acutæ* (2 pls) —O4, O4, 3 pairs
truncatæ (1 pl.) —O12, 1 pair

Pollen Counts. *acuta* (1 pl.).—Good 212, "inactive" 117, empty 235 (41.6 per cent), total 564

1933: 11 *E* (*r-lamarckiana* × *cockerelli*) (1930: 2, pl 11 × 1930: 7, pl 1)

Seeds germinated, 79 (79 per cent), ungerminated, 21 (11 with, 10 without embryo) total 100. Transferred to field, 30 plants (5 *gaudens elongans*, 25 *velans elongans*)

Velutina at first chlorotic, later becoming greener. Typical *velutina*, with red papillæ and pigmentation somewhat reduced by *elongans*, so that stems were but slightly reddened below and at tip, and bracts and cones were but lightly colored. *Elongans* caused wide flaring of bracts, appressed the pubescence on buds and stems, and reduced its amount, shortened the style, reduced petal size, and prevented flowers from opening flat. Leaves were moderate in

width, wavy, white midribbed, light greyish green. Central shoots absent, plants 1 m high.

Lata were typical, *gaudens* predominating in its effect on the phenotype. Red papillæ were lacking, as was pigmentation on stems, bracts and buds. Pubescence was scanty, but less appressed than in *velutina*. Bracts flared widely. Styles were shortened by *elongans*, petals were reduced in size, flowers failed to open flat. Fruits were shorter than in *velutina*.

Chromosome Configurations. *velutina* (1 pl.).—○4, ○6, 2 pairs *lata* (1 pl.).—○14.

Pollen Counts. *velutina* (1 pl.).—Good 400, "inactive" 4, empty 665 (62.2 per cent), total 1069
lata (1 pl.).—Good 400, "inactive" 2, empty, 473 (54 per cent), total 875

1931: 11 *Æ* (*muricata* × *cockerelli*) (1930. 1, pl. 9 × 1930: 7, pl. 1)

Seeds germinated, 16 (32 per cent), ungerminated, 34 (1 with, 33 without embryo): total 50. Transferred to field, 15 plants (all *rigens elongans*)

Plants 120 cm tall, with central shoots and short spreading laterals. Foliage was broader than in most *rigida*, and rather wavy-crinkled, especially above. Stems had very few long hairs, and hence few red papillæ, and were slightly reddened at tip; internodes not long. Bracts large. Buds green, stout, with appressed pubescence. Flowers small, self-pollinating. Fruits large.

Chromosome Configuration (2 pls) —○4, ○10

Pollen Count (1 pl) —Good 253, "inactive" 340, empty 236 (28.4 per cent), total 829

5. "Iowa 6" and its Hybrids

Æ. "Iowa 6"

Seed obtained through the kindness of Dr. A. P. Kelly. It was collected September 9, 1930, by J. B. Eisen in Dickinson County, Iowa, on the slope of a gravel pit, 1 mile southwest of Manhattan Beach. Cultures have been grown annually since 1932. Seed germination in successive years, 32 per cent, 66 per cent, 57.7 per cent, 75 per cent, 77.1 per cent.

Description.

Habit.—Plants 90 cm high with tall central shoot and low short rosette branches. Central shoots tend to lean or even to fall over under the weight of buds and foliage, particularly if late in developing, growing thereafter along the ground, this tendency less marked than in some other strains from Iowa.

Leaves.—Rosette leaves moderately narrow (e.g., 17×3 cm), somewhat wavy and crinkled, light greyish-green without pigmentation in midrib and margins, lacking red splotches, the marginal hairs appressed to the edge.

Stems with little color below, with green tips, and occasional minute red papillæ, long hairs sparse, fine felty pubescence present, giving a greyish caste. *Bracts* narrow, wavy, somewhat twisted in young tips, flaring widely, entirely green, spike truncate, crowded. *Buds* wholly green, ca 5.5 cm. long (cone and tip 2.5, hypanthium 2.25, ovary .75 cm), fairly stout, pubescence relatively short and somewhat appressed, only moderately abundant, sepal tips delicate, of moderate length, separating widely above, together at the base, not subterminal. *Style* of moderate length, stigma touched by anthers in ripe bud, self-pollinating; stigma lobes stout, long. *Petals* slightly broader than long, with shallow sinus. *Flowers* rather small (ca 4 cm. across) often failing to open completely, the sepals remaining attached near the tip. *Fruits* 4 cm long, rather slender, crowded.

Its two complexes differ but little in their effect upon the phenotype, as shown in reciprocal crosses. Both produce red papillæ, green stems (above and below); light green more or less wavy, uncrinkled, leaves of moderate width, with colorless margins and midribs, somewhat flaring bracts, green buds of moderate size, with appressed pubescence, short styles (flowers self-pollinated), moderately small flowers. Both complexes reduce, but fail completely to inhibit, stem, bract and bud color produced by other complexes.

Points at which they differ include the following

α Iowa 6 (transmitted through egg, rarely through sperm) shows less tendency toward central shoot formation, fails to inhibit stem color, even though it cannot itself produce it, produces lighter green foliage, the leaves being somewhat larger and more wavy, bracts larger, flaring more widely, bud cone longer, pubescence on cone less abundant, more closely appressed.

β Iowa 6 (transmitted through sperm) shows a strong tendency toward central shoot formation, inhibits stem color, produces light green but darker foliage than its associate, the leaves being smaller and less wavy, bracts are smaller, flaring but less widely, bud cone shorter, pubescence on cone more abundant, less closely appressed.

This form bears a closer resemblance to *cockerelli* than to any other form under cultivation, belonging therefore close to the *rydbergii-strigosa-subulifera* assemblage. It is one of several strains brought in from Iowa which resemble one another closely in phenotypic characters.

PLATE II

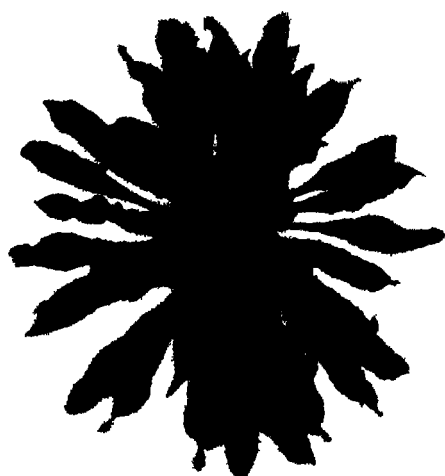


FIG 3 *Enothera* "Iowa 6," mature rosette



FIG 4 *Enothera* "Iowa 6 "

Chromosome Configurations.—Plants were examined cytologically as follows: 1932, 2 pls, 1933, 1 pl, 1934, 2 pls.; 1935 material collected not yet examined. All plants so far have shown $\bigcirc 14$. In each generation, after the first, culture has been grown from a plant whose chromosome configuration was tested

Pollen Count (2 pls.).—Good 400, empty 174 (30.3 per cent), total 574.

1934: 98 $\text{\textcircled{E}}$. ("Iowa 6" \times "Devil's Gate") (1933 52, pl 14 \times 1933: 40, pl. 2)

Seeds germinated, 104 (60.8 per cent), ungerminated, 67 (31 with, 36 without embryo): total 171 Transferred to field, 55 plants (α Iowa 6 \cdot Δ Devil's Gate).

Plants up to 125 cm., almost all lacking central shoot, rosette branches upright, tall α Iowa 6 modified Δ Devil's Gate effect in the following particulars. foliage and stems greyish with heavy felt, bracts flaring-recurved, buds wholly lacking in color, with heavy glandular pubescence, sepal tips spreading, not subterminal It failed to suppress the following Δ Devil's Gate characters pink mid-ribs, purple basal and tip coloration of stems, elongate character of inflorescence (mature buds far below tip of spike). From other crosses it is apparent that α Iowa 6 and Δ Devil's Gate are alike in producing rather broad foliage, green leaf margins, red papillæ, and in having a weak tendency toward central shoot production

Chromosome Configuration (2 pls) — $\bigcirc 4$, $\bigcirc 6$, 2 pairs

1934: 100 $\text{\textcircled{E}}$ ("Iowa 6" \times franciscana Sh) (1933 52, pl 3 \times 1933: 43, pl 13)

Seeds germinated, 50 (28.2 per cent), ungerminated, 127 (120 with, 7 without embryo): total 177 Transferred to field, 32 plants (α Iowa 6 \cdot Δ franciscana Sh.).

Plants uniform, 50 cm. high, without central shoots, lateral branches spreading α Iowa 6 could be seen to have the following influence. foliage made greyer, bracts shorter, smaller, more flaring, leaf marginal color suppressed, stem color reduced but not eliminated, long hairs and red papillæ reduced in number, bract and bud color suppressed or nearly so, bud pubescence appressed, spike made more elongate. Plants were intermediate in style length and flower size. Both complexes showed but a weak tendency toward central shoot production.

Chromosome Configuration (3 pls) — $\bigcirc 4$, $\bigcirc 8$, 1 pair

Pollen Count (1 pl) — Good 200, "inactive" 3, empty 241 (54.3 per cent), total 444.

1934 99 *Æ*. ("Iowa 6" \times *grandiflora*) (1933: 52, pl. 5 \times 1933: 47, pl. 10)

Seeds germinated, 85 (69 per cent), ungerminated, 38 (23 with, 15 without embryo). total 123. Transferred to field, 23 plants (6 α Iowa 6 *acutus*, 17 α Iowa 6 *truncatus*).

α Iowa 6 brings out the contrast between *acutus* and *truncatus* with unusual clarity

acutus. Plants bushy, 85 cm high, with central shoots. α Iowa 6 modified the effect of *acutus* in producing red papillæ, in reducing somewhat the size of long hairs, and hence of the papillæ, in appressing the long hairs, particularly on buds, in causing the bracts and sepal tips to flare noticeably, in somewhat shortening the style and reducing the size of the flowers. It did not prevent the development of a weak basal stem color or eliminate the fragrance of *grandiflora* blooms. Both complexes produce broadish light green leaves, which are but slightly wavy, and have white midribs, green margins and appressed marginal hairs; green stem tips, green bracts and buds. Plants when young were somewhat chlorotic. Iowa 6 plastids, therefore, find some difficulty in the presence of the α Iowa 6 *acutus* gene combination.

truncatus. Plants bushy, 120 cm. high. The influence of α Iowa 6 could be seen in the same characters as in the *acutus*. Red papillæ were few, owing to the *truncatus* tendency to reduce number of long hairs; basal stem coloration was brilliant, due also to *truncatus*. *Truncatus* was able to produce darker foliage, red midribs, narrower, wavier, brown-tipped leaves. Flaring of bracts was accentuated by α Iowa 6

Acutæ, in comparison with *truncatæ*, showed much longer branches when young, broader, lighter green leaves, and sub-erect bracts.

Truncatæ had shorter, redder stems, narrower, wavy leaves, flaring bracts.

Plants were typical *acutus* and *truncatus*, showing influence of α Iowa 6 principally in presence of red papillæ, appressed bud pubescence, accentuated flaring of bracts, and reduction in diameter of long hairs.

Chromosome Configurations. *acutus* (2 pls.) — $\odot 6$, $\odot 6$, 1 pair.
truncatus (2 pls.) — $\odot 4$, $\odot 10$.

Pollen Counts. *acutus* (1 pl.) — Good 200, "inactive" 5, empty 61 (22.9 per cent), total 266.
truncatus (1 pl.) — Good 200, "inactive" 1, empty 313 (60.9 per cent), total 514.

1934: 103 *CE*. ("Iowa 6" \times *oakesiana*) (1933: 52, pl 5 \times 1933: 35, pl. 1)

Seeds germinated, 183 (77 per cent), ungerminated, with embryo, 54: total 237 Seedlings were pale green and failed to grow. "Iowa 6" plastids were apparently unable to survive in the presence of the combined α Iowa 6 and *denudans* gene complexes.

1934: 101 *CE*. ("Iowa 6" \times *shulliana*) (1933: 52, pl 14 \times 1933 45, pl. 5)

Seed germination not recorded, but very high; 6 plants transferred to field (3 α Iowa 6 *maculans*, 3 α Iowa 6 *jugens*)

maculata Plants 80 cm tall, with central shoots and rather spreading rosette branches α Iowa 6 influence was seen in the following characteristics: spreading branches, moderate flaring of bracts and sepal tips, appressed character of long hairs on buds *Maculans* exercised a dominating influence on the phenotype, being wholly or chiefly responsible for central shoots, red midribs, bright basal stem color, sparsity of felty and glandular pubescence, and sub-erect bracts Bracts were intermediate in length Both complexes produce rather broad leaves, green stem tips, red papillae and green buds

jugata. Plants tall (120 cm.) with erect rosette branches *Jugens* and α Iowa 6 are alike in producing a lack of pigment in midribs, leaf margins, stems, buds, smallish flowers, appressed bud cone pubescence *Jugens* was responsible for tall central shoot, and α Iowa 6 for the light green foliage, sparsity of long hairs, waviness of cauline leaves and bracts, flaring of bracts and sepal teeth, elongated spike Leaf breadth intermediate Absence of red papillae correlated with sparsity of long hairs.

Chromosome Configurations maculata (3 pls).—O4, O4, 3 pairs

jugata (3 pls.)—O14.

Pollen Counts α Iowa 6 *maculans* (1 pl)—Good 200, "inactive" 3, empty 605 (74.8 per cent), total 808.

α Iowa 6 *jugens* (1 pl.)—Good 200, "inactive" 1, empty 157 (43.8 per cent), total 358.

1934: 111 *CE*. ("Devil's Gate" \times "Iowa 6") (1933: 40, pl. 2 \times 1933: 52, pl. 5)

Seed germination not recorded; 6 plants transferred to field

Plants 125 cm. tall, with central shoots (β Iowa 6) and tall rosette branches. β Iowa 6 expressed itself also in the suppression of

red color in midribs, reduction of red color on stems, flaring of bracts and sepal tips, greenness of buds, appressed character of long hairs. *Devil's Gate* brings out differences between α *Iowa 6* (see reciprocal, above) and β *Iowa 6* as follows: β *Iowa 6* has a stronger tendency toward central shoot production, reduces stem color more strongly, narrows and lengthens foliage, suppresses red midrib color, suppresses tendency toward waviness of leaves, causes bracts and sepal tips to flare. α *Iowa 6* does not develop a central shoot with *Devil's Gate*, allows more stem color, allows or causes broader, wavier foliage, allows red midribs, causes bracts and sepal tips to flare more widely, develops more abundant felt on stems and foliage, lengthens spike, has longer buds. Both complexes suppress bud and bract color. Neither carries a factor for red pigmentation of midribs, stems (except for red papillæ), bracts or buds.

Chromosome Configuration (3 pls.)— $\odot 4$, $\odot 4$, $\odot 4$, 1 pair

Pollen Count (1 pl)—Good 200, "inactive" 4, empty 177 (46.4 per cent), total 381.

1934. 116 *CE* ((*franciscana de V* \times *franciscana E* & *S*) \times "*Iowa 6*") (1933 29, pl 6 \times 1933 52, pl 3)

Seeds germinated, 23 (88 per cent), ungerminated, without embryo, 3 total 26. Transferred to field, 14 plants

Plants essentially uniform in appearance, with or without central shoots, rosette branches spreading widely, almost procumbent. β *Iowa 6* caused a reduction in stem color, very nearly eliminated cone color, entirely eliminated bract color, caused rosette branches to become more procumbent, gave compactness to the spike, reduced flower size, somewhat reduced pubescence on buds, and partially appressed it.

Chromosome Configurations—Two plants had $\odot 4$, $\odot 8$, 1 pair (*franciscana de V* β *Iowa 6*). Two plants had $\odot 4$, $\odot 4$, $\odot 4$, 1 pair (*franciscana E* & *S* β *Iowa 6*)

Pollen Count (1 pl)—Good 200, "inactive" 9, empty 181 (46.4 per cent), total 390.

1934 114 *CE* (*grandiflora* \times "*Iowa 6*") (1933.47, pl. 10 \times 1933 52, pl 5)

Seeds germinated, 85 (67.4 per cent), ungerminated, 41 (39 with, 2 without embryo), total 126. Transferred to field, 31 plants (18 *acutus* β *Iowa 6*, 12 *truncans* β *Iowa 6*, 1 metacline, *acutus* α *Iowa 6*).

acutæ. Plants 90 cm. high, bushy, with central shoots and rather spreading lateral branches. β *Iowa 6* contributed some

waviness to leaves, red papillæ, spreading sepal tips, it suppressed stem color almost entirely, reduced flower size somewhat, shortened style, so that flowers were self-pollinating. In most respects, the 2 complexes either agreed in their phenotypic effect, or else *acuens* predominated, so that in most respects the plants were typical *acuta*.

One *acuta* differed from the rest in possessing almost no side branches, and in presenting a decidedly depauperate appearance. It turned out to have an extra chromosome.

truncata. Plants 95 cm high, bushy, with central shoots and stricter, shorter lateral branches. β *Iowa 6* allowed the presence of midrib coloration, considerable waviness in foliage, it produced little modification of the *truncans* characters, except for forming red papillæ, and shortening style to a point where selfing occasionally occurred.

The distinctions between *acuta* and *truncata* were very marked.

One plant was a metacline (*acuens* α *Iowa 6*). It resembled its reciprocal in every particular (see above).

A comparison between reciprocal pedigrees shows clearly that α *Iowa 6* tends to differ from β *Iowa 6*, at least in the following ways: leaves wavier in the case of α *Iowa 6*, lighter green, bracts longer, more flaring, stems redder below, bud cones longer in relation to hypanthium, long hairs more closely appressed, sepal tips more flaring.

Chromosome Configurations *acuta* (3 pls).— $\bigcirc 4$, $\bigcirc 4$, 3 pairs
truncata (3 pls).— $\bigcirc 4$, $\bigcirc 8$, 1 pair
acuens α *Iowa 6* (1 pl.).— $\bigcirc 6$, $\bigcirc 6$,
 1 pair.

1934: 123 *E. (r-lamarkiana* \times "*Iowa 6*") (1933 56, pl 4
 \times 1933: 52, pl 3)

Seeds germinated, 13 (68.4 per cent), ungerminated, 6 (3 with, 3 without embryo) total 19. Transferred to field, 12 plants (2 *gaudens* β *Iowa 6*, 10 *velans* β *Iowa 6*).

velutina. Plants 55 cm high, mostly without central shoots. Characters were those usually imparted by *velans*, with the following noticeable modifications: bract and cone color almost entirely suppressed, long hairs on buds partly appressed, foliage somewhat reduced in size. One plant was taller, wavier, with shorter, stouter fruits, fewer papillæ and less color in stem. It proved to have 15 chromosomes.

latea. Plants were typical *latea*, showing little influence of β *Iowa 6*. The only noticeable influence was in the presence of red papillæ.

Chromosome Configurations. *velutina* (3 pls) — $\odot 4, \odot 8$, 1 pair.
late (2 pls). — $\odot 14$

Pollen Count *velutina* (1 pl) — Good 200, "inactive" 2, empty
 72 (26.3 per cent), total 274.

1934: 120 *CE*. (*nobska* \times "Iowa 6") (1933: 37, pl 7 \times 1933: 52,
 pl. 14)

Seeds germinated, 10 (83 per cent), ungerminated, 2 (1 with, 1
 without embryo). total 12 Transferred to field, 9 plants (2
pubens β Iowa 6, 2 *pubens* α Iowa 6, 5 *aenescens* β Iowa 6)

aenescens β Iowa 6. Plants 70 cm high, bushy. The influence
 of *aenescens* predominated, plants showing pink, crooked stems
 with curved tips, narrow dark green, flat foliage with strong marginal
 color and slightly pigmented midribs, green buds, with very short,
 broad cones, spreading pubescence and thick subterminal sepal tips;
 stout, short fruits β Iowa 6 seemed to induce sparsity of long
 hairs, it cut down stem and midrib color, and produced delicate
 red papillae

pubens β Iowa 6 and *pubens* α Iowa 6 Both β Iowa 6 and
 α Iowa 6 cut down the number of long hairs so much that red papillae
 were impossible to find Both were typical *pubata*, contrasting
 with plants containing *aenescens* in having green straight stems,
 broader, wavier, greyer-green leaves with white midribs and green
 margins; longer, more slender buds, with sepal tips not subterminal
 and appressed pubescence The plants with β Iowa 6 contrasted
 with those having α Iowa 6 in being lower of stature, with somewhat
 narrower foliage, more erect bracts, and buds somewhat hairier.
 All *pubata* were bushy, with central shoots (*pubens* β Iowa 6 = 70
 cm high, *pubens* α Iowa 6 = 85 cm.)

Chromosome Configurations *aenescens* β Iowa 6 (2 pls) — $\odot 14$.
pubens β Iowa 6 (2 pls) — $\odot 14$
pubens α Iowa 6 (2 pls). — $\odot 12$, 1
 pair

Pollen Counts *aenescens* β Iowa 6 (1 pl) — Good 200, empty
 395 (66.4 per cent), total 595
pubens β Iowa 6 (1 pl). — Good 200, "inactive"
 120, empty 773 (70.7 per cent), total 1093.

1934: 119 *CE* (*ostrea* \times "Iowa 6") (1933: 36, pl 12 \times 1933: 52,
 pl 3)

Seeds germinated, 48 (64 per cent), ungerminated, 27 (9 with
 embryo, 18 without). total 75. Transferred to field, 36 plants
 (*fascians* β Iowa 6)

In maturity, the typical plants were scarcely to be distinguished from *ostrea* itself, possessing the same distinctive characteristics of foliage and pigmentation (the stems were not nodding at the tips, but this character has largely disappeared in *ostrea* by maturity) Petals were often defective, variously cut, narrowed to nearly cruciate or frequently missing Apetalous flowers were not wanting The similarity between this culture and *ostrea* does not mean that β *Iowa* 6 and β *ostrea* are identical, but rather that *fascians* dominates the picture, for a general comparison of cultures in which β *Iowa* 6 and β *ostrea* are present shows that β *Iowa* 6 gives stricter plants than β *ostrea*, with greyer, shorter leaves which lack red splotches, with normal petals, and with sepal tips which are not subterminal, and stem tips that are not nodding

Three plants in the culture were aberrant. One of these possessed *fascians* characters in accentuated form, except that it had perfect petals. It was not fasciated. The other 2 plants were alike, but differed in the reverse direction from the typical, showing reduced pigmentation, greyer foliage, fewer papillæ, scantier pubescence, longer spike, petals were often defective All 3 aberrants were clearly *fascians* combinations The 2 plants that were alike might be metaclines (*fascians* α *Iowa* 6) in view of the reduced number of long hairs and the lengthened spike, however, one would expect from other crosses that α *Iowa* 6 would inhibit pigmentation less than β *Iowa* 6, rather than more Hence it can scarcely be assumed that these are metaclines It is probable that these plants represent crossovers (or possibly contaminations)

Chromosome Configurations Typical plants, *fascians* β *Iowa* 6 (2 pls) — $\bigcirc 14$

Aberrant with increased pigmentation (1 pl) — $\bigcirc 14$

Aberrant with decreased pigmentation (1 pl) — $\bigcirc 4, \bigcirc 10$.

Pollen Count. *fascians* $\cdot \beta$ *Iowa* 6 (1 pl) — Good 200, "inactive" 183, empty 119 (23.7 per cent), total 502.

1934: 92 \bigcirc (*shulliana* \times "*Iowa* 6") (1933: 45, pl 5 \times 1933-52, pl. 14)

Seeds germinated, 43 (82.7 per cent), ungerminated 9 (1 with embryo, 8 without). total 52. Transferred to field, 14 plants (11 *jugens* $\cdot \beta$ *Iowa* 6, 3 *jugens* α *Iowa* 6).

In general appearance, the metaclines (*jugens* $\cdot \alpha$ *Iowa* 6) resembled "*Iowa* 6" rather closely, while *jugens* β *Iowa* 6 looked more like typical *jugata*. The two complex-combinations showed contrasts as follows: *jugens* α *Iowa* 6 taller (120 vs 70 cm), with more

erect rosette branches, longer internodes; lighter green, broader, and relatively shorter foliage, which, especially near the apex, was more crinkled and wavy; bracts larger, flaring more widely, wavy-twisted; long pubescence on buds less abundant, more closely appressed, sepal tips flaring more widely; sepals thinner, hence flowers experiencing no trouble in opening (vs. *jugens*· β *Iowa* 6 in which flowers frequently fail to split open), later in blooming. Except for faint traces of basal stem coloration, none of the plants in either combination showed any red pigmentation.

Chromosome Configurations. *jugens* β *Iowa* 6 (2 pls.).— $\odot 4$, $\odot 6$
jugens α *Iowa* 6 (1 pl.)— $\odot 14$

The metacline examined showed the same configuration as that found in the reciprocally obtained α *Iowa* 6 *jugens* (vide supra)

Pollen Counts *jugens*· β *Iowa* 6 (1 pl.)—Good 200, "inactive" 2, empty 186 (48 per cent), total 388.

jugens· α *Iowa* 6 (1 pl.)—Good 200, "inactive" 6, empty 192 (48.2 per cent), total 398.

6. *Hybrids of nobska, ostrea and shulliana*

1934. 121 \odot (*nobska* \times *ostrea*) (1933. 37, pl. 3 \times 1933: 36, pl 12)

Seeds germinated, 34 (30 per cent), ungerminated, 79 (66 with, 13 without embryo) total 113. Transferred to field, 26 plants

All plants showed minute red papillæ, which suggests that they were apparently all *ænescens* β *ostrea*. Were it not for this fact they would probably have been called *pubata*. Lack of red mid-ribs and the bare trace of reddened leaf margins makes it a bit dubious as to whether the diagnosis is correct. β *ostrea* showed its influence in the narrow, long leaves, strongly reddened with age, and narrow, often defective to nearly cruciate petals. The plants had nodding stems and subterminal sepal tips, which characters are produced by both β *ostrea* and *ænescens*. The very short, stout bud cones (shorter than hypanthia) suggest *ænescens*.

Chromosome Configuration (3 pls.)— $\odot 14$.

Pollen Count (1 pl.)—Good 200, "inactive" 3, empty 402 (66.4 per cent), total 605.

1934: 122 \odot . (*nobska* \times *shulliana*) (1933. 37, pl. 3 \times 1933: 45, pl 8)

Seeds germinated, 122 (86.5 per cent); ungerminated, 19 (4 with, 15 without embryo) total 141. Transferred to field, 23 plants (3 *pubens*·*jugens*, 20 *pubens maculans*).

pubens jugens Plants ca. 75 cm. high, bushy, with central shoots. *Jugens* and *pubens* have very similar effects on the pheno-

type Plants were dark grey green, with narrow wavy foliage; stout buds with short appressed sepal tips and appressed pubescence; no red papillæ, an absence of red pigmentation on stems, bracts and buds, compact floral tips with spreading bracts Petals were often defective, or even missing. This is sometimes characteristic of other *jugens* combinations (*shulliana* × *ostrea*, *shulliana* × *Iowa* 6, *shulliana* × *franciscana* Sh)

pubens maculans. Plants 80 cm high, bushy, with central shoots *Maculans* showed a predominating influence, plants having red flecks on young leaves, red midribs, broadish, slightly crinkled, light green leaves, stems reddened below, green above, free from felty pubescence, red papillate, loosely constructed floral tips, green slender buds, with long delicate sepal tips, pubescence not appressed *Pubens* showed its presence mainly in increasing the amount of pubescence, including glandular hairs on the buds, which are absent in *maculans* combinations unless supplied by other complexes *Pubens* also reduced the *maculans* tendency toward the production of large numbers of small branches

Chromosome Configurations pubens·jugens (3 pls) —○4, ○8,
1 pair.

pubens maculans (3 pls) —○12,
1 pair

Pollen Counts pubens·jugens (1 pl) —Good 200, "inactive"
87, empty 1086 (79.1 per cent), total 1373

pubens·maculans (1 pl) —Good 200, empty 255
(56.0 per cent), total 455

1934: 104 *CE.* (*ostrea* × *nobska*) (1933 36, pl 12 × 1933 37, pl. 3)

Seeds germinated, 11 (73 per cent), ungerminated, 4 (1 with, 3 without embryo) total 15 Transferred to field, 9 plants

Plants uniform (all *fascians ænescens*), bushy, 75 cm high *Fascians* contributed the following red papillæ, pinkish color in pulvini and under side of midribs and proximal veins, especially in bracts (*ænescens* also has some tendency in this direction), pink cone color, with reddened ovary and bright red basal hypanthium color, somewhat appressed pubescence, reddened distal end of fruit; occasional absence of 1 or more petals; purpling of foliage when old (less noticeable than in many *fascians* combinations), occasional fasciation. *Ænescens* contributed dark green foliage color, red midribs; purple margins, especially in young leaves, nodding stem tips; spreading sepal tips (not, however, subterminal), broad petals. Both complexes contributed narrow foliage, reddened stems, small flowers.

Chromosome Configuration (5 pls.)—O 14.

Pollen Count (1 pl.)—Good 200, "inactive" 127, empty 215 (39.6 per cent), total 542

1934: 93 *CE* (*shulliana* × *nobska*) (1933: 45, pl. 5 × 1933: 37, pl. 7)

Seeds germinated, 11 (16 per cent); ungerminated, 58 (52 with, 6 without embryo) total 69. Transferred to field, 12 plants, all *jugens anescens*

This cross was made by Sturtevant (1931), but not described. Uniform, 50–70 cm tall, bushy, with central shoots (except in 2 plants), the stems irregularly bent in all planes, as is so often true of *anescens* combinations. Other *anescens* characters were: pink stems, dark green foliage, slight reddening of pulvini and (in case of bracts) lower surface of midrib and blade; reduction in number and size of long hairs, slight reddening of midribs, reddening of leaf margins in young leaves, nodding stem tips; short, stout bud cones, with thick, short, subterminal teeth. *Jugens* reduced midrib color, suppressed marginal leaf color, except in young rosettes, thickened sepals, so that flowers often failed to split open. Both complexes produce short styles and small flowers. *Fruit size* was intermediate

Chromosome Configuration (4 pls.)—O 10, 2 pairs

Pollen Count (1 pl.)—Good 200, "inactive" 22, empty 211 (48.7 per cent), total 433.

1934: 108 *CE* (*ostrea* × (*blandina* × *suaveolens*)) (1933: 36, pl. 12 × 1933: 3, pl. 7)

Seeds germinated, 44 (89 per cent); ungerminated, 5 (3 with, 2 without embryo) total 49. Transferred to field, 33 plants (14 *fascians flavens*, 19 *fascians blandina*).

Since *blandina flavens* has 4 independent chromosome groups in meiosis (O6, O4, 2 pairs), a certain amount of segregation is to be expected in progenies of this hybrid. Consequently, although *flava* and *blandina* could be distinguished in *ostrea* × (*blandina* × *suaveolens*), (confirmed by chromosome configurations), neither class was uniform in character. Plants were about 1 m. high.

Flava were bushy and lighter green, *blandina* usually had no central shoots, and were a greyer green. *Flava* showed variation in the following: length of buds and sepal tips (mostly stout, occasionally long and slender), size of red papillae, leaf breadth, cone and bract color (usually weak), hairiness. *Blandina* showed variation in bud size and color.

Chromosome Configurations *fascians flavens* (2 pls.) — 04, 06,
2 pairs

fascians ^{*h*}*blandina* (2 pls.) — 08,
3 pairs

Pollen Counts *fascians flavens* (1 pl) — Good 29, "inactive"
37, empty 102 (60.7 per cent), total 168.

1934 105 *OE* (*ostrea* × *franciscana* Sh.) (1933 36, pl 10 × 1933.43,
pl 13)

Seeds germinated, 18 (100 per cent) Transferred to field, 4
plants Seeds large, as in all hybrids with *ostrea* as ♀ parent

One plant was apparently a metacline (*β ostrea* ^{*h*}*franciscana*),
with narrower leaves and a chimeral arrangement of yellow and
green tissues It remained a rosette

Other plants uniform, without central shoots Characters
produced by ^{*h*}*franciscana* include broad, wavy foliage with trace of
red in midribs, marginal coloration, petals perfect, style long
Fascians caused brilliant purpling of older leaves, coloration of
young ovary, bright coloration of base of hypanthium and base of
cone, reddening of sepal tips, semi-appressed character of bud
pubescence, reduction in petal size Both complexes produce red
papillæ, stem, bract and cone coloration, slender buds. However,
the complexes tend to produce a different type and distribution of
stem, bract and cone coloration *Fascians* produces color which is
light magenta, and is found chiefly in base of stem, below the bracts,
in pulvini and under surface of bract midribs, in ovary, base of
hypanthium, base of cone and tips of sepal teeth The effect of
^{*h*}*franciscana* is to produce a strong, dark red or purple in the lower
stem, bright coloration of the stem tips (not merely beneath the
bracts), reddening of under surface of blade of bracts, uniform
coloration of cone, light but uniform coloration of hypanthium
The coloration of this hybrid was a blend of the effects of both com-
plexes, the distribution of color in buds, however, conforming more
to the *fascians* scheme

Chromosome Configuration (2 pls.) — 06, 4 pairs.

Pollen Count (1 pl) — Good 95, "inactive" 96, empty 448 (70.1
per cent) total 639

1934: 106 *OE*. (*ostrea* × *grandiflora*) (1933. 36, pl 10 × 1933. 47,
pl 10)

Seeds germinated, 50 (82 per cent), ungerminated, 11 (all with-
out embryo): total 61 Transferred to field, 40 plants (16 *fascians*
acuens, 24 *fascians truncans*) Seeds very large.

fascians acuens Plants bushy, with central shoots, 130 cm. high. *Fascians* was able to produce a slight reddening of the basal stem regions, also a slight pigmentation of pulvini, of the stems beneath bracts, of the under side of the proximal veins of the bracts, of the base of the hypanthia, base of cone (only occasionally), and tips of sepal teeth. In all regions, however, this pigmentation was weak. *Fascians* also produced red papillæ and strong reddening of older leaves, and appressed loosely the pubescence on cones. *Acuens* produced its characteristic upright bracts and loose floral tips, and suppressed the cruciate tendency of *fascians*, the petals being normal and all present. Flowers and fruits were moderately large, foliage light green.

fascians truncans. Plants bushy, with central shoots, 150 cm. high. *Fascians* produced red papillæ, slightly pinkish pulvini, a slight reddening below the bracts, slight reddening of underside of midribs, basal hypanthium color, occasional slight reddening of base of cones, strong sepal tip color, closely appressed bud pubescence. *Truncans* flattened the floral tips, causing bracts to flare, produced perfect petals, aided in causing bud pubescence to be tightly appressed. Flowers and fruits moderately large, foliage dark green.

The usual differences between *acuta* and *truncata* were clearly observed.

Chromosome Configurations *acuta* (3 pls) —○4, ○8, 1 pair
truncata (3 pls) —○14

Pollen Counts. *acuta* (1 pl.)—Good 200, "inactive" 35, empty 175 (42.7 per cent), total 410.
truncata (1 pl)—Good 200, "inactive" 172, empty 332 (47.1 per cent), total 704.

1934: 107 \bar{E} (*ostrea* \times (*r-lamarckiana* \times *blandina*) *lata*) (1933: 36, pl 12 \times 1933: 33, pl. 4)

Seeds germinated, 41 (68.3 per cent), ungerminated, 19 (4 with, 15 without embryo) total 60. Transferred to field, 37 plants (1 *fascians gaudens*, 1 dwarf rosette, possibly metacline; 35 *fascians-blandina*).

Fascians pigmentation characters showed strongly in hybrids with *blandina*, less strongly in *lata* (although present). Both showed some marginal color in leaves (especially *blandina*). Petals were perfect in all, red papillæ were present in all. Fruits were red-tipped in *blandina* hybrids, not in *gaudens* hybrid. Plants with *blandina* were 110 cm. high with central shoots. *Lata* was 60 cm. high.

Chromosome Configurations. *fascians*·*blandina* (3 pls) —○8,
3 pairs.

fascians gaudens (1 pl) —○6, 4
pairs

Pollen Counts. *fascians*·*blandina* (1 pl.).—Good 200, "inactive" 92, empty 454 (60.8 per cent), total 746

fascians gaudens (1 pl.).—Good 58, "inactive" 142, empty 938 (82.4 per cent), total 1138

1934 113 *OE*. (*grandiflora* × *ostrea*) (1933: 47, pl 10 × 1933: 36, pl. 12)

Seeds germinated, 63 (74.1 per cent), ungerminated, 22 (4 with, 18 without embryo): total 85. Of the 25 germinating seeds transferred to soil, 22 came up. There were 2 classes of seedlings, 11 of which were yellowish and 11 green. The former died early and were no doubt *acuens* β *ostrea*. The remainder were in some cases also slightly chlorotic, but recovered

truncans β *ostrea*. Plants 110 cm. tall, with central shoots and erect rosette branches. The influence of *truncans* was seen in the reddening of the lower part of the stems, the apparent suppression of the nodding stem character, the faint reddening of midribs, the flaring bracts, and large buds. β *ostrea* was most noticeably present in the brilliant red coloration of older leaves, the rather subterminal sepal tips, appressed pubescence, and the cruciate petals. Characters contributed by both complexes included narrow dark green leaves, green stem tips, absence of red papillæ, green buds.

Chromosome Configuration (3 pls) —○12, 1 pair.

Pollen Count (1 pl.).—Good 200, "inactive" 4, empty 280 (57.8 per cent), total 484

1934 126 *OE* (*muricata* × *ostrea*) (1933: 46, pl 4 × 1933: 36, pl. 12¹)

Seeds germinated, 52 (46.8 per cent); ungerminated, 59 (5 with, 54 without embryo). total 111. Transferred to field, 47 plants (*rigens* β *ostrea*).

Plants 1 m. high, very similar to *muricata* itself, but with defective (often cruciate) petals, more widely spreading bracts and foliage which developed anthocyan pigment when old

Chromosome Configuration (3 pls) —○14.

Pollen Count (1 pl.).—Good 200, "inactive" 165, empty 233 (39.0 per cent), total 598.

1934: 94 *Æ.* (*shulliana* × (*blandina* × *suaveolens*)) (1933. 45, pl. 8 × 1933: 3, pl 7)

Seeds germinated, 24 (82.7 per cent); ungerminated, 5 (1 with, 4 without embryo): total 29. Transferred to field, 21 plants (14 *jugens* · *^bblandina*, 3 *jugens* · *flavens*, 2 *maculans* · *^bblandina*, 2 *maculans* · *flavens*)

Distinctions between *jugata* and *maculata* clear, but those between *blandina* and *flava* less clear in case of *jugens* combinations, because of variation in the large class of *jugens* · *^bblandina* (due to presence of ○4, ○6, 2 pairs, in *blandina* × *suaveolens*). On the whole, *flavens* and *^bblandina* hybrids differed in the following: *flava* yellow green, less canescent, with flatter foliage, more acute floral tips, stems with long hairs only and no red papillæ. *Blandina* greyer green, with more crinkly and wavier foliage, broader floral tips with flaring bracts, red papillæ, and stems with both long and short pubescence.

jugens · *^bblandina*. Plants showed variation in the shape of floral tips (flat, broad, vs long, acute), in thickness of leaves, in foliage color (yellower vs greyer), and in presence or absence of pigmentation in bracts and buds. All these characters seemed to segregate independently. Plants 90 cm high. Stems greyish—downy, reddened at tip, with red papillæ, stout buds, coarse, semi-appressed pubescence. Foliage fairly broad, dark grey-green, wavy, crinkly, with midribs and margins uncolored.

jugens · *flavens*. Uniform. 80 cm. high. Foliage somewhat, but less, wavy-crinkly than in *jugens* · *^bblandina*. Red papillæ absent, long hairs present but no short hairs. Floral tips elongate, narrow, bracts bending inward, closely appressed to young buds. Buds green, with both types of hair (reduced in amount), stout.

maculans · *^bblandina*. Uniform. 70 cm high. Leaves broad, very wavy-crinkled, red midrib, rather dark green. Stems bright red below and at tips, with long and short hairs and red papillæ. Bracts green, flaring somewhat. Buds with slight traces of red in cones and no glandular hairs.

maculans · *flavens*. Uniform. 70 cm. high. Leaves broad, not wavy, although somewhat crinkled, red midribs, light green. Stems red below, green at tip, without felty pubescence, red papillæ present. Bracts bend in and press against young buds, green. Buds green, slender, without glandular pubescence.

Chromosome Configurations. *jugens* · *^bblandina* (3 pls) — ○12, 1 pair.

jugens · *flavens* (1 pl) — ○10, 2 pairs.

maculans ^h*blandina* (2 pls) —○10,
2 pairs

maculans *flavens* (1 pl) —○6, ○4,
2 pairs.

Pollen Counts. *jugens* ^h*blandina* (1 pl) —Good 200, "inactive"
2, empty 156 (43.5 per cent), total 358

jugens flavens (1 pl) —Good 200, "inactive" 3,
empty 104 (33.9 per cent), total 307

maculans ^h*blandina* (1 pl) —Good 200, empty
71 (26.2 per cent), total 271.

maculans flavens (1 pl) —Good 200, empty 133
(40.0 per cent), total 333.

1934. 96 *Æ* (*shulliana* × *franciscana* Sh) (1933·45, pl 8 × 1933·
43, pl 13)

Seeds germinated, 86 (91.5 per cent); ungerminated, 8 (1 with,
7 without embryo) total 94 Transferred to field, 40 plants
(3 *maculata*, 37 *jugata*) Sturtevant (1931) has described *shulliana*
× *franciscana* Em & St Their *franciscana*, however, differs from
ours in minor phenotypic characters.

jugens ^h*franciscana* Sh Plants 90 cm high, with central shoots
and widely spreading branches, ^h*franciscana* gave to plants a slight
basal stem coloration, red stem tips, red papillæ, long style *Jugens*
nearly suppressed basal stem color, completely suppressed bract and
bud color, thickened sepals so that flowers had difficulty opening,
appressed the abundant greyish pubescence Foliage wavy, mid-
ribs and margins uncolored, bracts flaring, flowers small. Petals
often somewhat deformed, truncate or narrow, semi-cruciate

maculans ^h*franciscana* Sh Plants 60 cm high, with central
shoots and widespreading rosette branches; ^h*franciscana* gave to
plants red-tipped stems, reddened bracts and buds Both com-
plexes produce basal stem coloration, red papillæ Flower size was
intermediate, as was style length *Maculans* produced broad,
crinkled foliage, with red midribs, it also reduced size of bracts,
caused them to stand erect, reduced felty pubescence on stems and
glandular pubescence on buds to a minimum Flowers had no
trouble in opening

Chromosome Configurations. *jugens* ^h*franciscana* (3 pls) —○12,
1 pair.

maculans ^h*franciscana* (3 pls.) —
○10, 2 pairs

Pollen Counts. *jugens* ^h*franciscana* (1 pl.) —Good 200, empty
97 (32.6 per cent), total 297

maculans ³*franciscana* (1 pl.) —Good 200, "inactive" 8, empty 87 (29.5 per cent), total 295.

1934-90 (*E. shulliana* × *grandiflora*) (1933: 45, pl. 5 × 1933: 47, pl. 8)

Seeds germinated, 105 (83.3 per cent), ungerminated, 21 (2 with, 19 without embryo: total 126. Transferred to field, 54 plants (19 *jugens acuens*, 28 *jugens truncans*, 1 *maculans acuens*, 2 *maculans truncans*, 1 aberrant with *truncans* and possibly a mixture of *jugens* and *maculans* chromosomes, 3 died).

jugens acuens Plants bushy, 120 cm. tall, with central shoots. Typical *jugata*, with little red pigmentation, narrow greenish foliage, appressed pubescence on stems and buds. In comparison with *jugens truncans*, foliage was lighter green, broader; bracts were more erect, broader, more loosely arranged, stems were slightly less reddened, and lateral branches were shorter. Midribs, leaf margins, stem tips, buds and fruits were without red pigmentation, basal stem color was exceedingly faint, red papillæ absent. Pubescence appressed on buds. Flowers quite large.

jugens truncans. Plants bushy, 135 cm. tall, with central shoots and shorter lateral branches. Foliage was darker green than *jugens acuens*, more wavy, narrow, bracts flared, giving broad, truncate spikes, stems had some, though not much red in the basal portion. Plants were devoid of anthocyan pigment except for traces in midrib (*truncans*) and lower stem surface. On the whole, plants of this combination resembled *jugens acuens* closely. Flowers quite large.

maculans acuens Plant bushy, low (75 cm.), very different from *jugata* in the light clear green (in fact semi-chlorotic) foliage with reddish midribs and red splotches when young, erect bracts whose tips press inward against the buds, resulting in a somewhat pointed spike, stems with bright red basal color, red papillæ and no felty pubescence, buds with erect long hairs, and practically no glandular hairs; narrower petals with deep sinus, shorter fruits. Stem tips and buds were green. These plants were clear examples of *maculans* hybrids, with their broad, thin, light green, red-flecked foliage, lack of greyness due to felty pubescence, erect bracts, clear green buds and stem tips.

maculans truncans. Plants bushy, 90 cm. tall, with central shoots. Typical *maculata*, but showing some differences from *maculans acuens*, to wit:—taller habit, shorter laterals, wavier, narrower foliage without chlorosis; bracts bending out slightly,

brighter red stems, slightly more short hairs on buds. Flowers quite large in all plants of this culture, whether *jugata* or *maculata*.

Chromosome Configurations. *jugens acuens* (4 pls.).—○8, 3 pairs (1 pl aberrant with ○10, 2 pairs).

jugens truncans (2 pls.).—○14

maculans acuens (1 pl.)—○10, 2 pairs

maculans truncans (2 pls.)—○14

Pollen Counts. *jugens acuens* (1 pl.).—Good 200, "inactive" 23, empty 172 (43.5 per cent), total 395

jugens truncans (1 pl.)—Good 200, empty 128 (39.0 per cent), total 328

maculans acuens (1 pl.)—Good 200, "inactive" 4, empty 170 (45.5 per cent), total 374

maculans truncans (1 pl.)—Good 200, "inactive" 1, empty 123 (38.0 per cent), total 324

1934 95 *Æ. (shulliana × r-lamarckiana)* (1933. 45, pl 5 × 1933 56, pl. 9)

Seeds germinated, 46 (92 per cent); ungerminated, 4 (without embryo): total 50. Transferred to field, 45 plants (11 *jugens gaudens*, 31 *jugens velans*, 1 *maculans gaudens*, 2 died early)

jugens gaudens Plants 120 cm tall, robust, with central shoots and spreading branches Typical *lata* They showed, however, the influence of *jugens* in the darkness of color, the greyness of stems, and appressed character of bud pubescence

maculans gaudens The single plant was also a typical *lata*, but, because of *maculans*, showed a lighter green foliage, red midribs, reddened basal stem regions, red papillæ, more erect bracts, unappressed bud pubescence Plant was bushy, but lower than the other *lata* (80 cm.).

jugens velans. Plants robust, with central shoots and tall laterals, 120 cm high Leaves narrow, dark greyish green, somewhat wavy, without anthocyan Stems greyish with red papillæ, but no other reddening. Bracts slightly reddened beneath, flaring slightly Buds slightly reddened on cones, with numerous appressed hairs of two lengths Fruits long Characters of *jugens* and *velans* were thus intermingled

Chromosome Configurations jugens-gaudens. — Sturtevant (1931) reports $\bigcirc 14$. (Confirmed)

maculans gaudens (1 pl.).— $\bigcirc 4$, $\bigcirc 6$, 2 pairs.

jugens velans. — Sturtevant (1931) reports $\bigcirc 12$. (Confirmed on 2 plants.)

Pollen Counts. jugens gaudens (1 pl) — Good 200, "inactive" 11, empty 338 (61.5 per cent), total 549

maculans gaudens (1 pl.).—Good 200, "inactive" 1, empty 72 (26.4 per cent), total 273.

jugens velans (1 pl) — Good 200, empty 232 (53.7 per cent), total 432.

1934 97 $\text{\textcircled{E}}$. (*shulliana* \times *muricata*) (1933: 45, pl 8 \times 1933: 46, pl. 6)

Seeds germinated, 51 (96.2 per cent), ungerminated, 2 (with embryo) total 53. Transferred to field, 20 plants, all *jugens-currans*. *Currans* characters were: tendency against central shoot production, basal stem coloration, narrow, wavy foliage with red teeth, long pubescence reduced in amount, stem tips nodding; sepal tips short, \pm spreading *Jugens* produced appressed pubescence Other characters were on the whole jointly produced by the 2 complexes—including green stem tips, absence of red papillæ, flaring bracts, green buds, rather short styles (plants self-pollinating), smallish flowers Very similar to *shulliana* \times *ostrea*, but with normal petals. Plants 70 cm tall.

Chromosome Configuration (3 pls.).— $\bigcirc 10$, 2 pairs

1933. 17 $\text{\textcircled{E}}$ (*shulliana* \times *oakesiana*) (1931: 72, pl 7 \times 1931: 71, pl 3)

Seeds germinated, 95 (95 per cent), ungerminated, 5 (3 with, 2 without embryo): total 100. Transferred to field, 29 plants (all *jugens denudans*)

Plants uniform, 85 cm high, with central shoots *Denudans* reduced pubescence so that leaves were nearly glabrous and stems were scantily clothed Buds were of the *denudans* type, green, almost hairless, with stout cones, narrow hypanthia, subterminal sepal tips. Floral tips were flat, the bracts spreading widely. Except for reddened marginal glands on leaves (*denudans*?) red pigmentation was absent. Foliage dark green below, yellowish

green at growing points (typical of *denudans*), wavy, toothed. Petals small, styles short.

Chromosome Configuration (4 pls) — $\bigcirc 10$, 2 pairs

Pollen Counts (1 pl.).—Good 400, "inactive" 5, empty 231 (36.3 per cent), total 636

1934. 91 *Æ. (shulliana × ostrea)* (1933: 45, pl 5 × 1933: 36, pl 12)

Seeds germinated, 28 (40 per cent), ungerminated, 42 (40 with, 2 without embryo) total 70. Transferred to field, 20 plants, all *jugens β ostrea*. Plants rather low (95 cm), usually with central shoots and widely spreading branches. Characters produced by *β ostrea* included nodding stem tips; somewhat spreading sepal tips, narrow to cruciate petals, abundant production of anthocyan pigment in older leaves. *Jugens* contributed greyish foliage and stems, and appressed pubescence. Both were responsible for narrow, dark green foliage, unpigmented midribs and margins, lack of red papillæ and stem coloration, greenness of buds and bracts, shortness of style.

Chromosome Configuration was not obtained, owing to failure to secure buds in the proper stage.

Pollen Count (1 pl) — Good 200, "inactive" 33, empty 180 (43.6 per cent), total 413

1934. 115 *Æ. (grandiflora × shulliana)* (1933: 47, pl 8 × 1933: 45, pl 5)

Seeds germinated, 85 (58.2 per cent), ungerminated, 61 (38 with, 23 without embryo) total 146. Transferred to field, 36 plants (15 *maculans acuens*, 17 *maculans truncans*, 1 *jugens acuens*, 2 *jugens truncans*, 1 aberrant).

Plants were undistinguishable from reciprocals (see above)

Chromosome Configurations *acuens maculans* (1 pl) — $\bigcirc 10$, 2 pairs.

truncans maculans (4 pls) — $\bigcirc 14$

jugens acuens (1 pl) — $\bigcirc 8$, 3 pairs.

jugens truncans (2 pls) — $\bigcirc 14$.

1934. 125 *Æ. (r-lamarckiana × shulliana)* (1933: 56, pl. 4 × 1933: 45, pl 8)

Seeds germinated, 93 (88.5 per cent); ungerminated, 12 (without embryo). total 105. Transferred to field, 68 plants (39 *gaudens maculans*, 9 *velans jugens*, the rest *velans maculans*)

The *gaudens maculans* and *velans jugens* plants were like their

reciprocals (see above). *Velans maculans* was absent in the reciprocal, but constituted the bulk of this family.

velans maculans. *Velans* contributed: waviness of foliage, weak tendency toward central shoot formation, red stem tips, red color on under side of bracts and on bud cones. *Maculans* was responsible for broad leaves, somewhat crinkled; red midribs, bright red color on lower half of stems, almost entire absence of felty or short pubescence in stems and buds, shortened styles. Both complexes produced red papillæ.

Chromosome Configurations. *velans maculans*. — Sturtevant (1931) reported $\bigcirc 12$, 1 pair, and this was confirmed on 2 plants
gaudens maculans (2 pls) — $\bigcirc 4$,
 $\bigcirc 6$, 2 pairs.

7 Miscellaneous Hybrids

1931 18 \mathcal{E} (*grandiflora* \times *chicaginsensis*) (1930: 16, pl. 2 \times 1930: 18, pl. 1)

Seeds germinated, 76 (95 per cent), ungerminated, 4 (2 with, 2 without embryo). total 80. Transferred to field, 30 plants (18 *acuens punctulans*, 12 *truncans punctulans*)

Plants tall, bushy, the differences between *acutæ* and *truncatæ* clearly observed. *Punctulans* contributed red papillæ, but failed to shorten styles. Flower size intermediate (4–5.5 cm.).

Chromosome Configurations. *acuens punctulans* (2 pls) — $\bigcirc 10$,
 2 pairs
truncans punctulans (2 pls) —
 $\bigcirc 10$, 2 pairs

Pollen Counts *acuta* (1 pl).—Good 217, “inactive” 9, empty 148 (39.5 per cent), total 374
truncata (1 pl).—Good 205, “inactive” 4, empty 694 (76.8 per cent), total 903

1932: 37 \mathcal{E} (*grandiflora* \times *suaveolens*) (1930: 16, pl. 1 \times 1930: 15, pl. 13)

Seeds germinated, 80 (80 per cent); ungerminated, 20 (5 with, 15 without embryo). total 100. Transferred to field, 30 plants (27 *truncans flavens*, 3 *acuens flavens*). *Acutæ* were chlorotic, but 1 plant managed to struggle through. *Truncatæ* were dark green. The usual differences between *acutæ* and *truncatæ* were noted.

Chromosome Configurations *acuens flavens* (1 pl.).— $\bigcirc 4$, 5 pairs.
truncans flavens (1 pl.).— $\bigcirc 14$.

1934: 128 (*Æ muricata* × *oakesiana*) (1933 46, pl 4 × 1933 35, pl 1)

Seeds germinated, 15 (83 3 per cent), ungerminated, 3 (without embryo) total 18 Transferred to field, 12 plants (all *rigens denudans*)

Plants similar to *muricata*, but with more tendency toward central shoot formation and bushy habit, more spreading bracts, stouter buds with scantier pubescence and more widely spreading sepal tips In other respects, the hybrid was practically identical with its maternal parent

Chromosome Configuration (1 pl) —○14

Pollen Count (1 pl) —Good 200, "inactive" 274, empty 230 (32 7 per cent), total 704

1931 12 *Æ (suaveolens* × *grandiflora*) (1930: 15, pl 15 × 1930 16, pl 1)

Seeds germinated, 102 (81 6 per cent), ungerminated, 23 (5 with, 18 without embryo) total 125 Transferred to field, 50 plants (8 *albicans acuens*, 5 *albicans truncans*, 36 *flavens acuens*, 1 *flavens truncans*)

This combination has been described by Gerhard (1929)

Chromosome Configurations *albicans acuens* (3 pls) —○10, 2 pairs

albicans truncans (2 pls) —○12, 1 pair

flavens truncans (4 pls) —○14

Pollen Counts *albicans acuens* (1 pl) —Good 220, "inactive" 199, empty 197 (32 per cent), total 616

albicans truncans (2 pls) —Good 346, "inactive" 427, empty 1407 (60 5 per cent), total 2180

flavens truncans (1 pl) —Good 243, "inactive" 7, empty 123 (33 per cent), total 373

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THE SONGS OF THE TODAS

M. B. EMENEAU

THE artistic activities of the Todas, a pastoral tribe of the Nilgiri mountains in south India, have been comparatively neglected in previous studies of their life and institutions. Indeed, Rivers¹ and earlier observers were of the opinion that they were deficient in artistic sense, Rivers in his chapter "Arts and amusements" devotes most of his space to certain realia of Toda life not included in other parts of his book, and to the arts (or fine arts) gives only passing mention. There are a few lines on the embroidery done by the Toda women; nothing is said of the ornamentation applied to wooden articles, such as walking-sticks and clubs; and the section on "Poetry and music" is meagre and in part incorrect.

The art of song among the Todas is highly developed and plays an extremely large part in their life. In comparison with it the art of story-telling is almost non-existent. In fact, imaginative story-telling hardly exists and the stories of traditional events in the life of the tribe do not seem to be popular. The tradition is there but is in the keeping of a very few men, and most members of the tribe either have never heard the stories or, not being interested, know them only in a garbled form. Some of the songs are based on legendary stories, but even in the case of these some of my informants knew the songs without knowing the stories. We seem to have a state of things where one art has been highly developed and practised to the exclusion of a closely allied

¹ Rivers = W. H. R. Rivers, *The Todas*, London, Macmillan and Co., 1906. I have treated the phonetics of the Toda language in a paper which will be published in *Language*. Some different characters are used in the present paper. [ō] represents the mid, mixed, rounded vowel. The retroflex consonants are represented by capitals, [ɽ], [ɽ], [ɽ], etc. [ɽ] is the one-flap tremulant, [ɽ] the post-dental trill. The combinations [ts, dz, tʃ, dʒ] represent the affricates, but when the two elements are separated by a period they are separate phonemes.

art It can be safely said that every Toda, man or woman, knows many songs and constantly amuses himself and others by singing either alone or with others Many of the songs are fairly old, the more popular of the large crop of new compositions of any given time surviving for many years, even until memory of the composer is lost There are at present nearly a dozen composers of note, both men and women, who have composed and are continually composing very prolifically. But many of the songs the words of which I have recorded are the work of persons now living who have to their credit only one or two compositions, one of them is the work of two small girls, who under the stress of homesickness were impelled by the pattern of their society to express their emotions as well as they could by inventing a tune and some fragmentary words The song was dictated to me by one of the most eminent of the composers, who, hearing the girls singing, completed the words and made a finished product of their attempt It has been said epigrammatically that in literate western society every person has within him one book; it can be said with even more truth that every Toda composes one song.² An indication of the popularity of the art is the rapidity with which newly composed songs become known to all the Todas They live in an area at least twenty miles long and ten miles wide, but when a song has been sung it will be known over most of the area within three or four days. Most of the Todas are continually on the move, visiting friends and carrying on their affairs over the whole area, and it seems that any new song is sung by anyone who has heard it in all the munds (*i.e.* Toda dwelling places) he may subsequently visit, and is thence carried to other munds by the members of this new audience One of the songs dictated to me had been composed only two days before by a person

² The Christian Todas of the agricultural colony formed by the Church of England Zenana Mission and nurtured by the devoted efforts of Miss C F Ling have had to cut themselves off from the tribe in almost all details But the impulse to song is very strong among them and they have their official composer who composes songs on all festive occasions It was to the credit of Miss Ling that during her time at the colony she made no attempt to suppress this strongly developed means of expression which survived when the tribal life was abandoned

in a mund at a distance of some fifteen miles from that in which my informant lived.

There are several types of song used by the Todas, their characteristics will be treated later in the paper. It is necessary first to give an account of the verbal structure, which is the same for all types of song. In singing, the verbal utterances are broken up into units of three syllables each (occasionally four or even five, rarely two). Each unit is generally an independent word. If the word in prose has only two syllables, in song it is eked out to fit the three-syllable scheme by augmenting a long vowel with a short anacrusis of the same quality ($V_1 > VV_1$), by interpolating a short vowel (usually [a] or [u]) into a consonant group, or by adding a seemingly meaningless syllable (most frequently [əd]) at the end of the word. Other methods are also found of attaining the desired number of syllables, but they need not be detailed here. In many cases the singing unit is made up of two words or of three, and frequently a compound word of prose is divided between two units of song.³ The units are grouped into phrases or sentences, running from one unit (generally a vocative phrase) to as many as six or seven. The usual length of the sentence is two, three, or four units; longer sentences are in general rather rare.

The most striking feature of the structure of the songs is that each phrase or sentence can occur only with a parallel phrase or sentence, so that the song as a whole falls into couplets. It is only in exceptional cases that one member of a couplet can be omitted. A further peculiarity, almost a corollary of the first, is that the pairs of units used in making up the couplets are rigidly prescribed by convention.⁴ The pairs are very often identical in meaning: e.g. each mund and

³ The language of song is somewhat different from that of speech. Differences are found in parts of the verb morphology, in the syntax which is frequently much looser than in prose, and in vocabulary. Many more words are borrowed from Badaga, Tamil and sometimes other sources in song than in prose, an example is the word for "snake," which in prose is [poib], but in verse most frequently [oif] from Badaga [hərvu] (the words are both related ultimately of course to Tamil [poimbu]).

⁴ Occasionally two pairs of sentences are interwoven, so that the first members of each are combined to form one couplet, the second members to form the second couplet.

each important place on the Nilgiris (stream, mountain, valley, grove, Badaga village, etc.) is referred to by its fixed pair of names, both of them usually being different from its ordinary prose name. The same is the case with the people of a mund division among the [toɪθaɔɪ], the other division of the tribe, the [təʃɪɪɔɪ], have no such pairs of names and can be referred to in songs only by other methods. The buffaloes of each mund division, of both halves of the tribe, have their pairs of names. These pairs of names for people, places, and buffaloes are called [kūasm]; Rivers (614-5) gives the [kūasm] of the [toɪθaɔɪ] and of the buffaloes, without seeming to recognize fully that they are pairs of words. An example or two will make clear how these pairs are used.

motsodfan	ur-ður xurj	uθfunum
buffaloes of [mɔɪɔɪ]	buffaloes-with joining	we are living
moɪðurθɛk	kor-ður xurj	"
buffaloes of [mɔɪɔɪ]	calves-with joining	"
poɪθɪ-k	noɪfɔɪxður	
mund [noɪs]-to	it is dawning	
θɪkɪj-k	koɪfɔɪxður	
mund [noɪs]-to	it is dawning	

The only frequent omission of one member of a pair occurs in the case of these pairs of names, especially those of the people of the [toɪθaɪ] divisions. If, as sometimes happens, all the [toɪθaɪ] divisions or the seven of them to the west of Ootacamund are being detailed, each may be represented by the first of the pair only, though in many cases in the songs in my material pairs are used.

Frequently the two parts of the pair have slightly different literal meanings, but in the context are taken to mean the same thing. An example is the reference to buffaloes and calves in the first couplet quoted. So also the two phrases for "it is dawning" in the second passage; both are somewhat obscure. The first apparently means "places-become light" or "places-(to)-becomes dawn", in the second the element [koɪ] is unknown otherwise, while the verb means "releases." Other examples:

pāidəθ-noɪr-k
 where we were born-place-to
 potsen-dəθ-k
 father's-god-to
 moɪj-wɪ-mox
 lap-in-children
 kəɪ-wɪ-xor
 calfpen-in-calves

puɪxum-θɪ
 let us go-rise up
 “
 “
 ʌɪwunum
 we have become
 “

This pair refers either to literal childhood, or to a state of helplessness as of children and small calves.

Many other pairs, each member with a different meaning, are fixed by convention for particular contexts.

kūaɪr-fuɪrfuɪs
 house-he has left
 kōɪr-θaɪrfuɪs
 pool-he has broken

uɪdətun
 they say
 “
 “

The pool is that made in the stream near a mund to supply drinking water. The pair in its context means: “They say that he is dead.” This is followed in one text by:

oɪr-θobaiɪj	aɪɪ-wɪɪ-art	θuɪwɪɪɪfɪwɪɪjaɪ
6-orphans	house-putting-shutting	have you run away?
oɪr-arkor	kəɪ-wɪɪ-art	“
6-orphan calves	calfpen-putting-shutting	“

Six is merely conventional for a largish number; the couplet means: “Have you left behind your children and calves uncared-for?”

In a description of a funeral come such pairs as:

kʉstə-θūwɪ
 such as was not built before-pen
 ɛɪjo-θɪɪj
 such as were not cut before-
 penposts
 kɔɪle-oɪr
 leg-dance

kʉstjɪθūwɪwɪ
 they are building
 ɛɪsɪθūwɪwɪ
 they are cutting
 oɪɪjθūwɪwɪ
 they are dancing

kone-nāwɪ	nāwɪxāwθwɪn
eyes-(for)-sights	they are looking at
peəkāwɪɾ-āwɪ	kāwɪxāwθwɪn
bier-with	they are carrying (the corpse)
pāwɪɾ-āwɪ	pāɪxāwθwɪn
accompanying buffaloes-with	they are driving (the buffaloes to be killed at the funeral)

In referring to a marriage:

nāɪnɪwɪ-n	nāɪθoɪɾ	iɪskitj-ʃn
mund [melgāɪ]-from	man of [melgāɪ]	mund [kāɪ]-from
nāɪ-mox-nāwɪɾj		pāɪxāwθwɪn
beautiful-wife-looking for		he is marrying
mūθfoɪð-ʃn	nāɪfep	iɪskfoɪð-ʃn
mund [melgāɪ]-from	man of [melgāɪ]	mund [kāɪ]-from
nāɪ-wɪɾ-nāwɪɾj		āɪxāwθwɪn
beautiful-buffaloes-looking for		he is receiving

Sometimes of course a conventional pair of phrases is appropriate in one context, but one member of the pair will be quite inappropriate in another. For example, [ðūmut·ʃxurb] "the Kurumbas in seven villages" and [ðūtāɪfysj] "the tigers in seven thickets" are the conventional pair for objects of fear, and are appropriate when a man has died of unknown causes in the jungle, or when someone is afraid, or in other contexts. But both are used (or their equivalents) even when it is a case of a man being killed by a tiger, or a person dying of the effects of Kurumba witchcraft. When Kurumbas are invited to attend a second funeral lasting for two days, the tigers also must be invited in song, though there is nothing further from a Toda's wish than to have tigers present at any festival, or anywhere else near him or his buffaloes. In one song composed by two men, describing a dream which each had had in which he made love to a woman, they sing:

ðɪ-xoɪl-oɪd	ersxāwθwɪn	koɪnomwɪn
eight-leg-goat	they are sacrificing	we do not see them now
mūtāθ-fuɪdʒ	kāwɪɪxāwθwɪn	"
pearls-worship	(the women) are giving	"

The pair is an adaptation of a riddle: [ɔrxoɬoɬɔɐj erjkin, mutaθfuɪdʒ kəwɪrkin] "I will sacrifice an eight-legged goat (i.e. I will kill a spider), I will do (lit give) worship with pearls (i.e. I will kiss her)." Only the second part is in point here. [mut] is the normal word for a pearl, but can also mean "kiss" (a borrowing from Badaga [mutɪə] or Tamil [mutɪam]), and this is the punning meaning ("they are kissing us") needed in this context. The "eight-legged goat," otherwise "spider," is quite out of place, but the composers kept it as a necessary part of the pair of phrases. That there is a limit, though a capriciously applied one, to the endurance of the misappropriate was seen when in a lament dictated to me the composer insisted on the omission of the second part of the couplet

kōɪr nɔθ-xuɪs	piəθɪk
funerals beautiful-making	you went to (i.e. conducted)
(i.e. beautifully)	
ponj nɔθ-xuɪs	"
work beautiful-making	you went to (i.e. did)
(i.e. beautifully)	

The second line has reference to cooking, carrying fuel, and doing other work at funerals, the man lamented was in fact so eminent that he did not do such work

A number of rather long setpieces are found in different songs. The phrases given above from a description of a funeral are merely part of a much longer passage which may occur in whole or in part in any lament. Variation in the composer's idea for the structure of the song as a whole will be reflected in the verb forms only, there will be differences of person, number, tense, etc. This passage may be used also with the appropriate variations in describing a man's prowess in catching buffaloes at a funeral, or in a song describing a quarrel at a funeral, or in a song about an Englishman who is interested in Toda institutions. In an interesting song composed by a man who had recovered from a severe illness, he uses the whole passage (as well as a further passage

in which all the landmarks on the road to the afterworld taken by a dead Toda and the buffaloes slaughtered at his funeral are enumerated) in couplets of the following form:

pauxoxon	ojuwsp-wk *	afuinen
dead	one who has become-like	I have become
oixnejn	oixox-wk-m	"
dead	one who has not become-	"
	like-also	
nity-wx-xois	wstjuwsp-wk	"
forehead-on-coin	one on whom they	"
	have placed-like	
koi-wx-xaig	kotoθ-wk-m	afuwsun
leg-on-black thread	those who have not	they have become
	tied-like-also	(or, it has become)
moixot-ñuwr	poduwp-wk	"
good clothes-with	those who have come-	"
	like	
moit-ñuwr	poiroθ-wk-m	"
good clothes-with	those who have not	"
	come-like-also	
perkñuwr-ñuwr	kñuwrwsp-wk	"
bier-with	those who carry	"
	(me)-like	
pañuwr-ñuwr	pañfoθ-wk-m	"
accompanying buf-	those who do not	"
faloes-with	drive-like-also	
	(buffaloes to be killed	
	at funeral)	

The details are all those of a funeral; the sense of each couplet is: "I have become as if I were dead in spite of all the reme-

* [ojwsp] is a "relative participle" of a form of conjugation which I shall call the "contemptual" [ojwspini] means "I became in spite of everything (my efforts, others' obstruction, promises, etc.)" In this passage the exact force is "in spite of all efforts to get well" [pauxoxon], [oixnejn] are the pair representing [kñuwr] of prose, the messenger who takes the dead to the afterworld, the analysis of the two words is obscure. In the following couplet, the coin is that placed on the dead man's forehead immediately after death, when his big toes are also tied together with black thread

dies I have tried; but at the same time I am as if I were not dead."

Another setpiece is found on the marriage of a man and a woman, detailing the buffaloes exchanged at the marriage, the salutations made by the couple to their new relations, the subsequent setting up of a house, birth of children, and prospering. Another has to do with a man of the [təufizjoɪ] becoming priest, conducting the operations of the dairy-temple, and prospering through the proceeds of the sale of ghee. Still another describes a boy's being hired out as a servant, taking care of the buffaloes and the children of the house in which he lives, running errands and doing housework. It is frequently combined with the preceding passage in singing of a man who from humble beginnings has become an important person in the tribe. Another describes the activities of the [noijm], or general meeting of the great men of the tribe to settle disputes. An interesting sequence of some poetical value is found in love songs. In it the suitor likens himself to the bee and his beloved to a flower. The passage in full is of some length, naming about a dozen different flowers and corresponding to each a different kind of bee. A specimen couplet is as follows:

per-fuf-oij	pustjũur	pe(ɾ)-rõin-oij	kũusaθeng
cane-flower-	if you blossom	cane-bee-	I have sucked
becoming		becoming	
kaɾ-fuf-oij	"	ka-θõin-oij	"
Strobilanthes-	"	black-bee-	"
flower-		becoming	
becoming			

Each of these sentences may be made into a pair with the meaning: "You have blossomed becoming like a flower, I have sucked becoming a bee." Other uses are found for this passage. In describing the catching of a buffalo at a funeral, the buffalo is said to be a flower and the man a bee. The most amusing use, certainly a parody in spirit, is in a song

about the bedbug In it the whole passage is adapted in this form:

kūwɨj-fuɨf-oɨj	puɨtuɨɨ-ɨɨd
Amaranthus-flower-becoming	he has blossomed-saying
kūwɨndɨɨn-oɨj	kūwɨsəθik
sp bee-becoming	you have sucked

It will be seen from the foregoing that there is little room for originality in Toda song. The set phraseology allows scope only in the adaptation of it to a slightly different set of circumstances from those of the last time it was used. There is hardly a pair of phrases that is not found at least twice in the material that I have collected. A further limitation is set by the convention that people must ordinarily not be named in the songs. In a lament the person will be indicated at the beginning and usually elsewhere in the song by the pair of [kūwɨm] of the people of his mund (and even this much is impossible in the case of a [təʔɨɨjɨɨ], though his mund can be named in the course of the song). Instead of the person's name the name of a buffalo is given to him and this is used throughout when it is necessary to indicate clearly that the person is spoken of. But this will not distinguish him from an actual buffalo, and frequently enough a buffalo will be involved in the incident about which the song is composed, context of course makes it clear which is man and which is buffalo. Even inanimate things, like honey or a railroad train, will be given a buffalo's name in songs about them. This absence of proper names and the conventional phraseology make it almost impossible for an outsider to have any idea of what a song is about, and in fact for the Todas themselves a song sung without a warning about its subject is almost unintelligible. As most songs are composed about incidents at the time and scene itself, no verbal warning is necessary. When they are repeated later, preface is necessary, as is the case with songs about events at which* the hearers were not present.

The convention that people should not be named is at

present being broken by [kainodz] (Rivers' table 21), probably the best of the composers. In a number of songs which he has dictated to me, he uses the name of the person sung about and claims great originality for this. His example seems to be followed by very few others at present, as he ruefully admits. His use of names is clever. In a lament for a man [piɔfoɔtoɔ], "silver-center plank in wall of dairy ([poɔtoɔ])," he puns on the name by creating another name [puɔfoɔtoɔ] "gold-center plank" and uses these two as a pair throughout the song. He has composed a lament for the death of King George V. The ordinary name for the late King would be [kiɔsoɔɔɔ]. This word means nothing in Toda, and in fact has in it a sound [ɔ] which is not a phoneme of the language. It suggests however [kinduɔ] "small" and, as [kainodz] says, is not poetical, consequently in the song it is given the form [siɔsoɔɔɔ], which suggests [sin] "gold."

In spite of all limitations however the composers treat of all sorts of subjects, even the most unpromising. The circle of interests peculiar to the tribe is fairly small, and the preceding account of the setpieces of phraseology indicates the major interests, funerals, marriages, dairy operations, sacred and profane, the prosperity of a man. The details of all these may be immensely varied—a man may be gored in catching a buffalo, a buffalo may be uncontrollably wild and its catching an act of great prowess, it may wander away from the mund and be thought of as saying farewell to the places it visits before it is killed at a funeral, a marriage may not be desired by the woman involved. Whatever the variation of detail, the composer can do the subject justice and frequently with much originality within the limitations set. More occasional incidents are also treated. When two dairies were being rebuilt some years ago and the ridgepoles were being brought with ceremony from the thicket where they were cut, one of the women composers sang a song in which the first pole to arrive at its destination announces the coming of the other along the way it must travel. Two women were prevented from going to a funeral and sang a song lamenting

their detention (in this the funeral setpiece was used). Two small girls were with their parents away from their own mund because of lack of pasture there for the buffaloes; in their homesickness they sang a song (see above). Two men sit on a mountain waiting for the women they love to come to them and while waiting sing and tell the birds to give their messages to the women of the munds. A woman after being divorced by her husband was bewitched by Kurumbas and died; on the night before her death she sang regretting that she had been put away by her husband and that she had gone to the festival where the Kurumbas were. There are numerous songs about things and events outside of the tribe. In one a Badaga girl is addressed who after a splendid marriage to which Todas were invited went part of the way home with her husband and then turned back to her parents. When Miss Ling, who was much loved by all the Todas (see note 2), left them to go to England, a song of farewell was sung at their leave-taking. There is a song still remembered about J. W. Breeks, who was collector in the Nilgiris about sixty years ago and is known for his archaeological and ethnological work. When Mr. C. F. Brackenbury, I. C. S., introduced the Toda Amelioration Scheme some years ago, a song was composed about it. When a planter was mauled by a tiger and died, a lament (put into the mouth of his mother, see below) was composed by some Todas who worked on his estate. Four songs have been composed about me and my asking questions about Toda affairs. When I had models made of a Toda house and of the [poit] form of dairy, a song was composed in which the Todas tell the models, addressed as buffaloes, to go and tell people elsewhere all about the Todas and the contents of the dairies. There is a song about the train, as was mentioned above. There is a lament for the late King George. These songs may be called lyric. Two that I have recorded suggest ballads in that they attempt to tell stories; one is about a quarrel at a funeral and the chief participants are named in successive sentences, abandoning the paired form. But their actions and the cause of the

quarrel can hardly be suggested, much less described. The other is the song about the Toda Amelioration Scheme mentioned above; a meeting is described and the advocacy of the Scheme by Mr. Brackenbury, but into his mouth are put many things which he did not say and would not have said, suggestions for many social changes which, advocated by missionaries, were mixed up in the song by the tribal traditionalists with the economic changes initiated in the Scheme. The relating of events in accurate detail is almost impossible in the songs; the convention allows only hints at them which are understood by the hearers.

A curious class of songs is those dreamed by people. They are apparently fairly numerous, but I have only four in my material. One of these was dreamed by a man who is regularly a composer, the other three were dreamed by people of whom I have not discovered that they have ever composed songs. Of these two were women and the other a man. In all four songs and in all others that are dreamed, so I am told, the sleeper sees a person or persons who have recently died and hears them singing. In two of the songs the singers were two men who lamented that they had died young and before they had lived life fully. In the third a woman appears and apostrophizes her husband who is intending to marry again, she says that she will not allow the second marriage but will take him with her to the afterworld; if he was told of the dream by the woman who saw and heard it, it did not deter him from the marriage. The woman who dreamed this song woke up in the middle of it and the song is incomplete. In the fourth a woman who had recently died after bearing a son lamented that she could not give her child a mother's care. This song also was broken off when the dreamer woke; he at once waked all the people in the mund and sang the song to them. The fact that two of these songs were dreamed incomplete and that they were not completed disposes one to think that little, if any, conscious addition has been made to the dreamed songs, though a conscious tampering might have proved difficult in the case of the incomplete songs,

owing to the unusual nature of the subjects and the lack of proficiency in composing of the dreamers

One class of songs not hitherto mentioned is about legendary events, such as the coming of the original buffalo to a [tɪ] dairy, or the creation of various creatures in the beginning. Others of this class are about gods, but so conventional in phraseology that little definite emerges from them that would be intelligible without explanatory accounts. These songs belong mostly to the type called [pɔɪɾ], about which more will be said below

The songs are divided by the Todas themselves on the basis of the manner of delivery into two divisions, those which are composed and delivered during dancing, and those which are sung without dancing. The latter are again subdivided on the basis of the type of tune into three divisions.

The dancing of the Todas is very familiar to visitors of the Nilgiris and has been described often enough, though never very clearly. Only men dance. They form a circle facing inward to its center, each man's hand being joined to that of his neighbor in such a way that, with elbow close to side and forearm at right angles to upper arm, the palms of the two men's hands are together and the fingers interlaced without being bent. The circle then rotates in counter-clockwise direction with a measured tread, the right foot of each man at each step being placed behind the left foot of his right-hand neighbor and then the left foot brought across to the front of the neighbor's right foot. Most of the dancing is done to the accompaniment of a concerted shout [o haʉ haʉ], which marks the time for each step. To almost all gatherings where there is to be dancing, one or two composers are invited. At the present time, [tɪɾɪxɪwɪɾ] of [tɔɪɾɔɪɾ] (Rivers' table 20) is the foremost of these composers for the dance, another is [pɪwɪwɪ] of [mɛɪɪɪ] (table 45); I have frequently seen these two men working together. After a dance of the type just described, the circle breaks up and after a short rest is reformed. The composer forms one of the circle; if two men are composing together, they are side by side in the circle,

the chief one being on the left of the other. The circle then rotates in somewhat slower time than in the dance just described and after a few preliminary shouts of [haü haü] by the whole circle, the composer shouts the first three-syllable unit. If he has a companion composer, the first syllable of the first unit will give him his clue to what is to come and he will shout the remainder of the unit with the leader. Since the words are rigidly conventionalized, all the rest of the couplet will then be known to the assisting composer. For the next couplet he will await the clue, and so on. The leader may adhere strictly to turns of phrase that are standardized for the various types of festival—marriage, funeral, setting up of first planks at rebuilding of dairy, thatching of dairy, etc., or he may attempt some original turn. After each unit is shouted (in a peculiar throaty bark which distorts the consonants and the vowels and makes the words quite unintelligible to anyone but a Toda), the whole circle shouts it in unison. Then three or four men on each side of the composers shout [haü haü] and the whole circle repeats it. This is repeated for each unit until the end of the words is reached. The circle then breaks up. The composers for these dances are specialists. They must know all the names and [kūasm] connected with each mund and dairy, belonging to such things as the contents of the dairies, stones, trees, milking-grounds, watering-places, pens, calf-sheds, and the like. [täifxüwü:R]'s memory for these things is phenomenal and must be the result of long apprenticeship and practice. [pu:stüwü:]'s is not of such high standard, he seems to be still in the apprenticeship stage, but in addition composes the other type of song, which [täifxüwü:R] does only very rarely.

Songs which are sung are divided into three classes, according to the type of tune. The tune is more important than the words; as one of the composers remarked to me, anyone can compose words, but an original tune is a more difficult thing. I know of one song of which the tune was composed by two men and the words by a third, and another (mentioned above) of which the tune and some words were composed by

two girls and the whole was finished by a third person. The largest class of songs is the [nõũ];⁶ it can be composed and sung by anyone. One sub-species of [nõũ] is named [orɽjfoj] "which (he, she, they) lamented," *i.e.* a lament. Such songs are in the form of a lament by some relative of the deceased person, or persons, they are usually composed however by one of the regular composers and may be sung by anyone. [kãmodz] has recently made an innovation by composing a lament in which two persons, the husband and the sister of a woman, are represented as singing after her death. Whether this original touch will become popular remains to be seen.

The [poɽɽ] cannot be sung by women and of course should not be composed by women. I have recorded two specimens of [poɽɽ] which were composed by women, but it is recognized that these were exceptional cases. One is the song mentioned before, sung by a woman the night before she died as a result of Kurumba sorcery. The other was composed by the women in the shelter at a two-day funeral when a man who was gored by a ferocious buffalo was put in with them before he was carried to Ootacamund to a hospital. A great many of the [poɽɽ] are those songs mentioned before, which have to do with legendary events and the gods, and it may be that these very sacred matters should not be sung of by women. But not all songs with this subject-matter are [poɽɽ], and others of the [poɽɽ] class differ not at all in subject from the [nõũ], in fact, I have a specimen which is [poɽɽ] when sung to one tune and [nõũ] when sung to another. The third class is

⁶ This word means "noise," then "voice" as in [and ũwɽjɽnõũmɽ] "his good-voice-is," *i.e.* "he has a good voice"; or "tune of song, song" as in [nõũɽwɽ-] "sing a song," lit. "song-make," or [pundõũɽwɽ-] "compose a song," lit. "new-song-make." The word [poɽɽ], used only for this type of song, has an allied verb [poɽɽɽɽ] "he is singing a [poɽɽ]," [poɽɽwɽ] "he is not singing a [poɽɽ]." The words of any song, including the dance-song, are called [kow]. The pair used in songs for "song" is [sũwɽɽɽwɽ], [sũwɽɽnõũ] "pair-words, pair-tune." Another way of referring to the pairs of phrases is seen in the following sentence, where one man is arranging the method of singing with another, he to take the first half of each couplet, the other man the second half [mudũɽɽɽwɽ ōɽkɽn, pydũɽɽɽwɽ ōɽɽ] "first-words I will say, after-words say." The verb most generally used with [kow] is this verb "say, tell," when an old song is being repeated, when a new song is being composed, a usual expression is [kowɽwɽ-] "words-make."

[tim]), sung by the women when they are pounding grain; it is not sung by men for obvious reasons.

When a man sings he will whistle the tune to himself first, and then begin to sing in a vocalised growl. The tune is repeated over and over without variation. Various tunes differ in length, but as far as my untutored observation goes, most are short and will accommodate only one unit of three syllables preceded and followed by a number of syllables the only content of which is a vowel on which to modulate. Women's singing follows the same pattern, but their voice production is much shriller and very nasal. They generally cover the mouth when singing, making the whole performance very indistinct. When several people sing together, the preliminary whistling assures that all shall know the tune, and the words are known in the same way as in the dancing. The singing of several people is sometimes in unison, sometimes antiphonal. It should be noted that Toda music is a subject still to be investigated; it would well repay study. It may be allied to the music of the other tribes of the Nilgiris, though superficially it seems to have as little connexion with that as with the music of the plains people of south India.

The texts of Toda songs are interesting in themselves as a help to the understanding of the pattern of Toda life. But beyond this, they have a more general interest. Studies have been made of oral epic and the technique of the stereotyped phrase used in all such epic, whether Homeric, Sanskrit, Finnish, or South Slav. In Toda songs we have a lyric of a peculiar allusive type in which the only technique is that of the stereotyped phrase, or rather of a stereotyped parallelism of phrase. The Vedic hymns show the use of similar technique in lyric,⁷ though there is no systematic parallelism of phrase and though the re-use of phrases is much more sporadic, as it is in the epics which have been studied. For parallelism of phrases, we must turn to Hebrew poetry, though

⁷ See M. Bloomfield, *Rig-veda Repetitions*, and the three volumes on Vedic variants, especially Bloomfield, Edgerton, and Emeneau, *Vedic Variants*, Vol. 3.

there the process is much more free, and the use of the stereotyped phrase is very limited. If we combine the Hebrew parallelism and the use of stereotyped phraseology of the epics or the Vedas, and push the combination to its farthest point, we have Toda poetry

YALE UNIVERSITY

**JOINT MEETING OF THE AMERICAN PHILOSOPHICAL
SOCIETY WITH REPRESENTATIVES OF FOUNDATIONS,
SOCIETIES, UNIVERSITIES, AND INSTITUTIONS,
ADMINISTERING FUNDS IN AID
OF RESEARCH**

FEBRUARY 19 AND 20, 1937

REPRESENTATIVES and guests from the following organizations were present:

American Academy of Arts and Sciences

Edward M. East, Chairman Permanent Science Research Fund

American Association for the Advancement of Science

J. McKeen Cattell, Chairman Executive Committee

George A. Birkhoff, President

Forest R. Moulton, Permanent Secretary

American Council of Learned Societies

Waldo G. Leland, Permanent Secretary

Donald Goodchild, Secretary for Fellowships and Grants

American Museum of Natural History

Clark Wissler, Dean Scientific Staff

G. Kingsley Noble

American Philosophical Society

Roland S. Morris, President

Edwin G. Conklin, Executive Officer and Vice-president

William E. Lingelbach, Secretary

Alfred N. Richards, Committee on Research

Arthur W. Goodspeed, Editor

The Bartol Research Foundation of the Franklin Institute

W. F. G. Swann, Director

Boyce Thompson Institute for Plant Research

William Crocker, Director

University of California

Charles B. Lipman, Dean of the Graduate Division

Carnegie Corporation of New York

Frederick P. Keppel, President

Carnegie Institution of Washington

John C. Merriam, President

Oscar Riddle

Albert F. Blakeslee

562 JOINT MEETING OF RESEARCH ORGANIZATIONS

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Richard P McKeon, Division of the Humanities

Columbia University

Marston T Bogert

Franz Boas

The Franklin Institute

Henry B Allen, Director

Geological Society of America

C R Longwell, Chairman Projects Committee

H R Aldrich

John Simon Guggenheim Memorial Foundation

Frank Aydelotte, Chairman Educational Advisory Board

Harvard University

Donald Scott, Director Peabody Museum

University of Illinois

Roger Adams, Professor and Head of Department of Chemistry

Indiana University

Edwin H Sutherland, Head of Department of Sociology

Johns Hopkins University

Edward W Berry, Dean

David M Robinson

Lalor Foundation

C Lalor Burdick, Secretary

Josiah Macy, Jr, Foundation

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Fred E Wright, Home Secretary

National Research Council

Albert L. Barrows, Executive Secretary

E R Long, Chairman Division of Medical Sciences

University of Pennsylvania

Detlev W Bronk, Director of Eldridge R Johnson Foundation
for Medical Physics

Edward P. Cheyney, Chairman of Faculty Committee on
Research Grants

H S Oberly, Secretary of Faculty Committee on Research Grants

Conyers Read

Princeton University

Luther P Eisenhart, Dean of the Graduate School

William B Scott

Solomon S Lefschetz

Edward Capps

Rockefeller Foundation

Warren Weaver, Director for the Natural Sciences

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C G Abbot, Secretary

Aleš Hrdlička

Social Science Research Council

Robert Treat Crane, Executive Director

University of Virginia

S A. Mitchell

Wesleyan University

H B Goodrich

University of Wisconsin

E B Fred, Dean of Graduate School

PROGRAM

Friday, February 19, 10 A M - 5 P M

ROUND TABLE CONFERENCE

EDWIN G CONKLIN, Vice-president of the American Philosophical Society, presiding.

The discussion of some or all of the following subjects was proposed:

- 1 Grants-in-aid as distinguished from fellowships and scholarships.
2. Relative emphasis on projects and men
- 3 To what extent should administration endeavor to seek out promising projects and men?
4. How best may reliable information be secured as to the merits of projects and the competence of applicants?
5. For what specific purposes should grants be made? *e.g.*
Salary of applicant
Travel and maintenance

564 JOINT MEETING OF RESEARCH ORGANIZATIONS

Assistance, technical and clerical

Exhaustible supplies

Equipment of lasting value, *e g.*—apparatus, books, MSS, etc, and their ultimate disposal

- 6 Desirable size limits of grants-in-aid Should they be generous or limited to necessities?
7. Under what circumstances should grants be renewed, and should renewal be so frequent as to constitute continuous assistance?
8. What oversight or control should be exercised over the use of grants, the expenditure of money, the progress of research?
- 9 What have proved to be the most effective administrative device for bringing systems of grants-in-aid to the attention of scholars, for handling applications, for assuring careful study of applications by experts and committees, and for making awards
10. Is it desirable to promote large projects by relatively small grants from many sources?
11. Are prizes, whether competitive or honorary, an important means of promoting research?
12. Is it desirable to effect a better coordination among the various agencies that offer grants-in-aid, either as to the size of grants, the fields in which they are offered, or the overlapping of applications? What has been their distribution among fields of study and among grades of scholars?

Friday Evening 8.15 o'clock

PUBLIC LECTURE by FREDERICK P. KEPPEL, President of the Carnegie Corporation, New York, on "The Responsibility of Endowments in the Promotion of Knowledge"

Saturday, February 20, 10 A.M.—1 P.M.

OPEN SESSION



ROLAND S MORRIS, President of the American Philosophical Society, presiding.

General Topic:

**"The Most Important Methods of Promoting Research,"
As viewed by Representative of**

1 Research Foundations and Institutions

John C. Merriam, President of the Carnegie Institution of Washington

Warren Weaver, Director for the Natural Sciences, Rockefeller Foundation

2 Learned Societies, Academies and Councils

Waldo G Leland, Permanent Secretary of the American Council of Learned Societies

3. Universities, Professional and Technical Schools

Alexander G. Ruthven, President University of Michigan

Frank Aydelotte, President Swarthmore College

4. Research Workers and Recipient Institutions

Edward P. Cheyney, Chairman Faculty Committee on Research Grants, University of Pennsylvania

Detlev W. Bronk, Director Eldridge R. Johnson Foundation for Medical Physics, University of Pennsylvania

ROUND TABLE CONFERENCE

FEBRUARY 19, 1937

INTRODUCTORY REMARKS OF EDWIN G CONKLIN,
Vice-president of the American Philosophical Society.

It is a pleasure to welcome to the American Philosophical Society, which is a shrine of science and learning, as Independence Hall is of patriotism, the representatives of some thirty-five organizations that are engaged in the administration of funds in aid of research. Mr. Waldo G. Leland, Permanent Secretary of the American Council of Learned Societies, suggested the appropriateness of this oldest learned society in America serving as sponsor for this meeting and he has aided in preparing topics for the conference and has agreed to open the discussion this morning.

Every organization represented at this meeting has its own peculiar problems and methods and there is no possibility or desire to unify all practice in promoting research, but we do desire to learn from the experience of others what methods have been found most useful. In order to insure free and frank discussion no reporters or stenographers are present. But lest this meeting justify the title, "Gone With the Wind," I ask those willing to do so to send me later abstracts of their remarks for publication in the *Proceedings* of the Society. In this way we may hope to have a permanent record of an important conference. Some eight or nine years ago, so I am told, a conference somewhat similar to this was held but it was decided not to pass any resolutions nor to make public any results of the conference. We do not expect that any resolutions will be adopted at this meeting but if those who take part in the discussion will later furnish outlines of what they would or could or should have said, rather than of what they did or did not say, it will constitute the best possible record of the thoughts stimulated by this conference.

Of the organizations represented here several are great foundations or institutions with enormous resources and it is to be expected that they would in general prefer to distribute funds for research through intermediate organizations rather than directly to numerous individual workers. Mr Carnegie once said that he preferred not to engage in the "retail business" of philanthropy, and Daniel C Gilman, first president of the Carnegie Institution of Washington, spoke in this very room in 1902 and 1903 of the difficulties of distributing funds to really worthwhile men and projects. He said, more or less facetiously, that of the many applicants for funds about one third were cranks, one third professional beggars and only one third modest scholars with genuine needs. In part, no doubt, as a result of this difficulty of handling numerous individual applications the Carnegie Institution of Washington has established in various fields research institutions of its own, through which in large part it operates. On the other hand the Rockefeller Foundation has generously endowed existing institutions and has called into being research councils, that in turn take care of the "retail business" of distributing grants and fellowships. Such a federation of great foundations and intermediate distributing organizations which are better able to deal with specific sciences or individual workers seems to be a very satisfactory way of supporting projects and persons that are most worthy, and of encouraging promising but relatively unknown investigators. The American Association for the Advancement of Science, with its small research fund, has distributed a portion of this through the State Academies of Sciences, thus reaching many worthy but relatively unknown workers who would otherwise have had little assistance or encouragement in their work.

Much could be said in favor of small grants to earnest workers in small colleges, since such institutions are the chief source of supply of graduate students and research workers in the larger universities. The universities are primarily educational and only secondarily research institutions. But they are and must ever be the chief source of research workers.

Therefore, they have particular need of fellowships and scholarships. Even when fellowships and scholarships are supported by great foundations the persons appointed generally work in the stimulating environment of universities. Many universities also have research funds for the support of the work of the members of their faculties or of advanced students. The administration of such funds usually has the advantage of intimate personal acquaintance with applicants, but also the disadvantage of being limited to members of one institution and of departmental or personal pressure in making awards.

Some twelve topics have been proposed for discussion in this round table conference. I think it is desirable that these should serve merely as suggestions and that the persons present should not feel bound to limit their remarks to these topics nor to take them up in the precise order in which they stand in the program, but that each should feel free to speak out of his own experience "as the spirit moves him," which is an appropriate proceeding in this Quaker City.

I call upon Mr. Waldo G. Leland, Permanent Secretary of the American Council of Learned Societies, who has kindly consented to open the discussion at this conference

WALDO G. LELAND For some years the three major councils (National Research Council, Social Science Research Council and Council of Learned Societies) have administered substantial funds, contributed by the Rockefeller Foundation, for grants-in-aid of research awarded to individual scholars to assist them in meeting the expenses of specific investigations. In an increasing number of universities special research funds have become available, from budgetary sources, from endowments, or from gifts, for the same purpose, and awards from these funds are periodically made to members of the faculties of those institutions. A few societies and academies have also been able to make similar awards in modest amounts. The American Philosophical Society, among such organizations, has large funds at its disposal

for this purpose, and has devoted much attention to the problem of administering them in the best possible manner

In view of the multiplicity of funds for grants-in-aid, and of the variety of ways in which they are administered, it has been thought useful to invite those who have had experience in their administration to meet in conference for the purpose of giving critical and objective consideration to grants-in-aid as a means of promoting research.

1. It is first necessary, however, to agree upon the subject of the discussion, and the following definition of grants-in-aid, and its accompanying statement of their objectives, are offered as a first step towards such an agreement. The definition corresponds to the practice of the major councils—National Research, Social Science, and Learned Societies—which have administered substantial funds, provided by the Rockefeller Foundation, for this form of assistance to research.

Definition. A grant in aid of research is a subvention to an individual to assist in meeting the expenses of a specific project of research. It is distinguished from a fellowship in that the latter is chiefly educational in purpose.

Objectives. The ultimate objective of grants-in-aid is the advancement of knowledge, either directly by contributions of new knowledge or indirectly through the better organization of present knowledge, the preparation of necessary tools, and improvement of methods and techniques, and through experimental or exploratory operations. Grants-in-aid may also have objectives with respect to research personnel, such as the discovery of aptitudes, encouragement of research, and the improvement of environment by making it more conducive to research.

2. As the above statement of objectives indicates, emphasis is placed both on the project for which assistance is asked and on the man who applies for aid. The project must be practicable and its expected results must be useful; the man must be at least of presumed competence. The councils,

however, (though I am of course speaking only for the Council of Learned Societies) have not hesitated to make speculative awards of a few of their smaller grants, being glad to take a chance on scholars who seem to have promise but who have not been able to demonstrate their superior ability or even their competence. They have hoped in this way to discover or to bring out qualities which may become a valuable addition to the scholarship of the country.

3 The Council of Learned Societies, while using due diligence to make its system of grants-in-aid known, and while frequently passing around, or causing to be passed around, suggestions that applications might appropriately be made, has not made any systematic search in the field for likely applicants. The modesty of the funds at the disposal of the Council and the lack of sufficient staff have made intensive field work impossible. But the Council has relied a great deal upon its constituent societies, through their officers and delegates, to find for it the most promising cases.

4 The problem of passing upon applications is largely a matter of securing reliable opinions and information about the applicant and his project. The appraisal of the project does not offer great difficulty, for objective and competent opinions as to the intrinsic—and what is perhaps more important, the relative—value of specific undertakings should be readily obtainable. It is important, however, not to be afraid to assist projects which, because of their novelty, may not command support from the usual sources of opinion. In judging applications, imagination must have its proper part. What is more difficult is to secure really objective appraisals of the applicant's competence. Recommendations too often have to be taken at a liberal discount; in the course of time an accumulation of information respecting recommenders makes it possible to establish the discount rate of each.

5 The conception of grants-in-aid of research as contributions to the expenses of research excludes their use for the salary of the recipient, and also for normal living expenses. But what about compensation for loss of salary that would

have been received for teaching in summer time? And what about grants for the purchase of the applicant's time through the employment of a substitute? Such matters should be the subject of negotiations between the applicant's university and the granting body, for the university may, in clearly meritorious cases, reasonably be expected to participate in the assistance, at least to the extent of making concessions as to teaching schedules

Such uses of grants as helping to meet the expenses of travel and maintenance (above normal living expenses) in the field of technical and clerical assistance, and of obtaining exhaustible supplies, are clearly indicated, and present little difficulty, but the ultimate disposition or ownership of durable objects, such as books, photographs, apparatus, etc., presents at least a problem. The Council of Learned Societies expects that such materials shall be placed at the disposition of other scholars when the grantee no longer needs them. Books, manuscripts, and photographs may appropriately be placed in a library, the Council's only experience with important apparatus has been with the use of a machine for the electrical recording of sound, which has been employed in linguistic research. This machine was built for a grantee, but the Council retained ownership of it, and after the grantee had completed his work with it the machine was loaned to other scholars who had need of it.

6. It is believed that grants-in-aid should be of rather modest amounts. The Council of Learned Societies has awarded 351 grants totaling \$138,000, with an average value of \$393. The extreme range has been from \$100 to \$2,000, the present limit is \$500, and most grants are of \$300-\$400. Assistance to a large number of men and projects, instead of concentration upon a few, is more consistent with the purpose of a system of grants-in-aid, which is to distribute encouragement as widely as possible.

7. It is important to insist upon the fact that the award of a grant is a single transaction and that the awarding body does not incur the slightest degree of responsibility, moral or

otherwise, for assistance beyond the amount awarded. Assistance to, not support of, research is the purpose of grants-in-aid. Applications for renewals of grants should be regarded as new applications, and must take their chances in the competition in which they participate

8 While the Council does not exercise any oversight or control over the use of grants or the conduct of the research for which they are awarded, it does require "a brief report showing the mode of expenditure of the grant and the scientific results obtained through its aid," and grantees are expected to deposit with the Council copies of publications resulting from the assisted research. About 65 per cent of the grantees have complied with these requirements, and their reports have made it possible to make some estimate of the utility of the system. One hundred and nineteen grantees have reported 188 publications, ranging from short articles to works in several volumes. Nearly all the publications are useful; some are important, some are of unusual significance.

Any appraisal of the value of the system of grants must also take into account a good many intangibles. What has been its effect upon the intellectual morale of American scholarship? Has it improved the environment of research? Has it, being applied on a national scale, tended to equalize opportunity between the scholar in the institution which has no research funds and the scholar in the institution which has such funds? A study of the distribution of the grants of the Council of Learned Societies shows that grants have been awarded to members of the faculties or staffs of 113 institutions, including a few museums and libraries, while nineteen awards were made to scholars having no academic positions at the time of their applications. The great majority of the scholars thus aided had access to no other source of assistance. In all cases of applications from members of institutions maintaining research funds, careful enquiry was made as to why the desired assistance could not be had from university funds. The grants have also been well distributed among the various disciplines and studies of the humanities, and have

aided in the development of several of the so-called "under-worked" fields.

In conclusion, it may be said that the Council of Learned Societies, speaking for the scholars in the humanities, is convinced that its modest system of grants-in-aid, in operation since 1926, has been one of its most useful activities, that it has stimulated scholarship and improved its environment, and that it has amply justified itself. The Council believes, however, that any such system must be operated with watchful care; it cannot be administered mechanically, abuses must be avoided, improvements must be constantly sought.

FRANK B. JEWETT, Chairman of the Milton Fund Committee of Harvard University, was unable to be present but sent the following statement.

As to the results of my experience after twelve years as Chairman of the Milton Fund Committee of Harvard, I think these can be summarized in a very few words. Further, I think my conclusions are not different from the conclusions of those who have served on the Milton Fund Committee and, so far as I know, of those who have had somewhat corresponding experience on similar committees or boards.

Briefly stated, my feeling is that the most profitable way to use money available for the stimulation and support of research is to concentrate on finding men who, after subjecting their record to every examination which it is possible and feasible to make, commend themselves as being A-1 research men, and then to appropriate money for their support or the support of whatever projects they think important. The basis for this is the assumption that really good men are not likely to concern themselves with essentially second-rate problems. On the other hand, first-rate men in a particular field are in a better position than second-rate men in that field or first-rate men in some other field, to judge whether or not a problem is potentially promising.

A corollary to this is that a first-rate problem in the hands of a second-rate man is a doubtful thing in which to invest money. In connection with the hundreds of applications for

grants-in-aid which have been before the Milton Fund Committee during the past decade, there have been many research problems which, as problems, not only commended themselves to the Committee but were likewise certified as important by leaders in the particular field involved, but for which the Milton Fund Committee made no allocation of funds. This was because we could not satisfy ourselves that the person presenting the request was capable of attacking the problem effectively

Of course we have had numerous cases in which both the man and the problem he suggested were clearly first-rate but for which we did not recommend a grant-in-aid. Most of these cases, however, were cases in which we had every reason to believe either that the investigator was well past the prime of his creative productivity or that for some reason or other he could not continue on the problem for a sufficient length of time to produce adequate results

Personally I am very skeptical about the ability of group organization for the purpose of planning real worthwhile research attack on major problems except in certain limited and more or less obvious directions. History, it seems to me, indicates pretty clearly that the really great advances have resulted from individual accomplishment. One might almost say, I think, that these advances and the new fields which have opened thereby are the result of a sort of inspiration which has come to qualified individuals.

The exceptions where progress through organized planning of research can be anticipated are, it seems to me, confined generally to two major fields in both of which the problem for solution is large and more or less obvious to a considerable number of qualified and interested men

(1) One of these fields is what might be termed the field of engineering research, in which the main problem is made up of a large number of substantial but more or less independent problems, all of which must proceed with some degree of uniformity if the final solution is to be expedited. In this case the problem is really that of agreeing upon a division of the

field and allocating the several elements to those most qualified or most interested to handle them.

(2) The other exception which occurs to me is in a way somewhat analogous and is exemplified, for instance, in the field of astronomy and I think in certain problems in the biological and medical sciences where organized cooperative attack by qualified men is indicated as the best method of procedure.

W F. G. SWANN, Director of the Bartol Foundation of the Franklin Institute, raised the question of the relative values of fellowships and grants-in-aid, and spoke of the distinguished accomplishment of the fellowships program of the National Research Council, which had been the chief factor in bringing the state of research in physics in this country from a position distinctly behind that of European physics to one of world leadership. If, then, the relative importance of fellowships and grants-in-aid is germane to the discussion, Mr. Swann's opinion was that the fellowships are incomparably more valuable

KARL T. COMPTON, President of the Massachusetts Institute of Technology, seconded Mr Swann's endorsement of the great stimulus and advancement of science in America which came from the National Research Fellowship program, and believed that this program should be continued

It is natural however that relative emphasis as between fellowships and financial support of projects may change. Obviously the first step in building up scientific strength in the country is to train scientists as was done by the Fellowship program With these scientists in action in increasing numbers, the problem of finding ways and means to support their research becomes of increasing importance, and this feature I believe justifies some retrenchment of the Fellowship program in order that the support of research through grants-in-aid may be more effective.

Along with the outstanding success of the National Research Fellowship program, there appear to be some minor but real difficulties There was some question as to whether there

were not more fellowships than there were really first class outstanding candidates. Some of the fellows supported for two or three years by these fellowships during the time when they would normally have been establishing themselves in a remunerative position showed evidence of an unfortunate attitude of feeling that the world owed them a living or a feeling of superiority to some of their confrères—equally able—who were carrying a heavy share of the burden of teaching and other academic duties. There is also a continual problem of the placement of men at the termination of their fellowship period.

These problems have suggested the desirability of modifying the fellowships to something more of a coöperative arrangement between the Fellowship Board and the University to which the fellow is assigned. To this end I submitted a year and a half ago to the Association of American Universities a plan for post-doctorate fellowships according to which the institution would contribute a portion of the stipend and would receive in return not over six hours per week of teaching services. In this way the fellow would have an opportunity to work into the affairs of the university in such manner as to lead to his later employment if circumstances justified this, and in any case it would give him teaching experience and a sense of responsibility for academic duties. This plan however was criticized largely on the ground that it would be difficult for institutions to postpone their plans for teaching schedules to a time as late in the academic year as that at which National Research Fellows have ordinarily been appointed.

Finally, on the question of the importance of men *vs.* projects, it is my judgment that the two can never be separated, and must both be considered in the award of a grant. There is evidence of the unfortunate results of the extreme policy of picking out a man and supporting him through life on the one hand or of voting funds in support of projects without attention to the men available to prosecute them on the other hand.

One aspect of the situation which has impressed me greatly has been the surprising manner in which new fields of research are opened up by young men who have been practically unknown and are in unexpected places, and I believe that a grants-in-aid program for research will be most effectively administered if its administration is sufficiently alert and flexible to find these important new projects and men as they appear

MARSTON T. BOGERT of Columbia University, representing research in chemistry, stressed the need of post-doctoral fellowships to enable professors doing research to have trained assistance such as is available to European scholars.

ROGER ADAMS of the University of Illinois, while agreeing with Mr Bogert upon the need of such assistance, emphasized the necessity of assisting younger men to their own independent research careers. Money, therefore, should be available to younger men for assistance or for a reduction of teaching loads, in order that they may quickly develop as independent investigators, rather than as technical hands for older scientists

ALBERT F BLAKESLEE of the Carnegie Institution for Experimental Evolution wondered if our various grants committees are doing the greatest possible service in confining their allotments of funds to those who apply. It is conceivable that some method of inquiry might be devised which would discover researchers in support of whose work a grant would pay good dividends but who would not be caught by merely scanning the list of applicants and their accompanying recommendations

This is illustrated by our experience on the council of the American Institute for the award of medals of which Mr Compton and Mr. Bogert were also members. The scheme at first was for the council to receive nominations, each of which was sponsored by three persons. Naturally the sponsors spoke in glowing terms of the scientific attainments of their candidate. In more than a single instance in my own field the same man acted as sponsor for two different candi-

dates without offering any comparison between their merits. It became evident that the kind words of sponsors who were requested to write eulogies were of little value in helping us to select a man worthy of an Institute medal. The committee finally decided to pick its own sponsors and to make them advisors. At a preliminary meeting of the council those nominees that were obviously ineligible were eliminated from further consideration. For each of those that remained and of those that were newly proposed by the council we selected three specialists, not necessarily members of the Institute, as advisors who were asked to rank the candidate in comparison with others in his special field and in addition to list in order of merit the leading three men in this field. The response from the advisors was very gratifying. We had expert judgment on our candidates, but there was another advantage to the scheme. In certain cases the advisors convinced us that there were particular persons more worthy of a medal in a given field than the candidate about whom we had sought advice.

I am aware that awarding grants on the basis of written applications with accompanying documents is a method which recommends itself from its relative ease of administration. I believe, however, that some committees on grants—that of the American Philosophical Society, for example—might find it profitable to experiment with some such scheme as that adopted by the American Institute's council on awards. They might find that their yield in scientific dividends would be increased over the present plan of depending solely upon those who make personal application for funds.

WARREN WEAVER, Director for The Natural Sciences of the Rockefeller Foundation, speaking unofficially but from the point of view of the Foundation, reverted to the subject of definition of grants-in-aid, accepting that proposed by Mr. Leland and further defining the size of such grants, as administered by the Foundation. In that organization, grants-in-aid are limited, in the case of the American office, to a maximum of \$7,500, and in Europe to a maximum of \$3,000.

He distinguished further between two types of administration of grants-in-aid. 1) those cases in which a grant-in-aid program, as a relatively isolated activity of some organization, is essentially an end in itself, and 2) cases of organizations, like the Foundation, which have broad general programs of which the grant-in-aid is a functional part, used primarily for the purpose of serving the general objectives of the Foundation. As an illustration of the fact that there will inevitably be a difference in procedure in these two instances, he indicated that, in the Rockefeller Foundation's activities in The Natural Sciences, relatively few grants-in-aid are made for the purpose of completing small research projects, while some handle temporary or emergency aspects of general program items, and others are used for the early exploratory stages of projects which might at a later time develop into major undertakings.

Mr Weaver warned against too rigid separation of projects and personnel, although agreeing that excellence of personnel is a first and prime consideration. As between ideas and things, the investment in imponderables almost always proves the more substantial. He cited as an example the case of the Mathematical Institute at Gottingen. While the investment in the building itself could not now be viewed with the utmost satisfaction, nevertheless the Foundation has reason to be gratified with the results of its investment in men in connection with this undertaking.

He referred also to a change in the application of criteria since the prosperous years of the twenties. At that earlier time it was possible practically to exercise only one criterion, that is, of outstanding excellence. Since then, however, the reduction in available funds has necessitated certain limitations in scope, and the Foundation has found it wise to concentrate upon certain sectors of the scholarly horizon. Within these sectors, of course, excellence remains the primary consideration; and, indeed, considerations of outstanding excellence still warrant occasional excursions into areas which, as a whole, are not now being actively cultivated.

Referring briefly to the subject of fellowships, Mr. Weaver said that it was the opinion of some of the officers of the Foundation that the recent policy of retrenchment, entirely understandable in view of the changed situation in this country and in view of the very great financial magnitude of the preceding program, had perhaps been carried somewhat too far

Mr Weaver, in response to a comment of Mr. Birkhoff, mentioned a type of fellowship to which the Foundation has given some attention. These may be designated as cooperative fellowships. They would, for example, be made possible by diminishing contributions from the organization administering the fellowships and by increasing contributions from universities. They would be designed to diminish the teaching load of young scholars at that time in their careers when they should be active in research and frequently are not because of other responsibilities.

FRANZ BOAS of Columbia University called attention to the training value of grants in support of long-continued projects. Adducing the example of research carried on in American native languages, he showed that persons associated with this work had received training of a high order, but that such results could not be accomplished through short-lived projects.

After a brief recess, Mr. Conklin called upon Mr. ROBERT T. CRANE of the Social Science Research Council for comments. Mr. Crane mentioned the relative ease with which fellowship programs could be financed, and the difficulty encountered in raising money for grants-in-aid. He described the policy of the Social Science Research Council as tending to limit its assistance to the completion of projects. That Council places the emphasis primarily on the men who are engaged in the projects, but this does not imply that the recipients of grants are necessarily the best men in the country in their several fields. This is in some measure explained by the fact that such men are frequently able to secure the necessary assistance from the universities.

Mr. Crane mentioned the high overhead cost of administering the grants-in-aid of the Social Science Research Council, and expressed his emphatic opinion that this cost was justified by the results. The cost is due to the Council's effort to see the work going on in the universities and to get at first hand from research workers and experts the best available opinions concerning research under way

ALBERT L. BARROWS, Executive Secretary of the National Research Council, reported that the National Research Council has followed several methods for the utilization of research funds in the natural sciences which have been placed in its hands by the foundations, and by industrial corporations and other agencies. Chief among these uses is the support of fellowships, mainly of post-doctorate grade, about 1,100 having been appointed during the past seventeen years. The Council has also administered funds for special purposes, which have been used according to programs prepared by committees of the Council set up for each project. In addition the Council has administered certain funds in its capacity as fiscal agent only for other organizations without assuming responsibility for the scientific program or work of these organizations. The Council has also had the administration during the past eight years of a general research aid fund from which comparatively small grants have been made (averaging about \$600 each) in response to individual requests. The sums expended through the Council under these several plans since the permanent organization of the Council in 1919 are approximately as follows

Fellowships	\$4,070,000
Special projects	3,175,000
As fiscal agent	1,487,000
Individual grants-in-aid	377,000
	<hr/>
	\$9,109,000

Specific benefits are to be derived from each of these modes of using money in the support of scientific work. The returns coming from investments in fellowships probably reach further into the future than the results from any other

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method and are multiplied in many ways. Funds expended according to a cooperative program under the guidance of a committee or of a permanent organization bring results of a definite nature through contributions to knowledge and by increasing the capacity of institutions for research in these selected fields.

Much is to be said also for the utilization of a certain amount of money through grants of moderate sums for the encouragement and assistance of individual investigators under conditions of emergency, for the encouragement of men in remote institutions and the assistance of men in institutions of limited means, for the aid of important projects and competent men in the absence of other available resources, and for exploratory purposes leading to the recognition of able investigators and of timely projects and of trends of research in various fields. By means of these grants the abilities of men and the various resources of the institutions at which they are located may to a certain extent be capitalized for increased advantage in the progress of research. The experience of the National Research Council has led to the belief that, when utilized without displacing institutional responsibilities for the support of research, there is an advantageous and important place for the expenditure of funds through individual grants-in-aid of research. Scientific and educational institutions have for many years, in fact, been committed to this method as one of the obvious means for the encouragement of scientific work.

Mr Conklin then described to the conference the method employed by the American Philosophical Society in administering its grants-in-aid through its Committee on Research, which meets five times a year. He exhibited copies of blank forms of application and of announcements of the general principles adopted by the Committee as follows:

- 1 Grants will be made only for the promotion of research and chiefly in the fields represented by the Membership of the Society.

2. Grants will not be made to pay salaries of members of the staff of an educational or scientific institution. It is also expected that such institutions will cooperate by furnishing general laboratory, library and office facilities for those engaged in the investigation.

3. Grants will not be given for the support of professorships, fellowships, or scholarships, nor in general for work on doctoral theses. They will not be given for usual or permanent equipment and special apparatus of permanent value purchased by means of a grant shall become the property of the Society and shall be liable to recall when the purpose for which it was purchased has been fulfilled.

4. Projects, methods of procedures, places where the work is to be done, and any cooperation of other institutions or agencies should be clearly stated.

5. Preference will be given to the support of investigations which are already well begun and in which definite results can be expected with the aid of the grant.

6. All publications of work supported in whole or in part by a grant from this fund shall state in connection with the title that the work was supported by a grant from the Penrose Fund of the American Philosophical Society, and at least a summary of the work shall be offered to the Society for publication in its Proceedings.

7. As a general policy the funds allocated to each project shall be disbursed quarterly by the Society to those in charge, unless the nature of the work requires a different arrangement.

8. Reports of expenditures from grants are expected at the close of each quarter, and a report of progress should be made by the grantee to the Committee on Research semi-annually.

9. No recipient of a grant shall thereby become an employee of the Society.

LAWRENCE K. FRANK, Assistant to the President of the Josiah Macy, Jr., Foundation, advanced the opinion that a considerable part of the funds used for research are not devoted to the promotion of significant projects, that they are absorbed by routine activities and that much of the research undertaken with their assistance is obsolete before it starts. He indicated the necessity of focusing grants-in-aid where they would really advance human knowledge, and considered one of the dangers attendant upon grants-in-aid in their rela-

tion to the proper coordination of research in the universities. As an example, he cited a hypothetical case in which an anatomist needs the assistance of specialists in other fields of work. Because the other departments of his university cannot or will not contribute their expert services, the anatomist is obliged, by means of grants-in-aid, to hire specialists. In such a case, it is fair to raise the question whether grants help or hinder the proper development in the universities of coordination and cooperation between departments.

MR. LELAND directed the discussion toward the problems of selecting recipients of grants-in-aid. The questions are, how to find the men, who should be supported, and how to rate them. He asked whether the comments of experts in the universities provided adequate and reliable information.

SOLOMON S. LEFSCHETZ, Professor of Mathematics, Princeton University, strongly favored the administration of funds through the universities, where the selection of recipients could be made on the basis of long and intimate acquaintance. He opposed the necessity, inevitably associated with other methods of awarding grants, of passing judgment on his fellow scientists on the basis of inadequate acquaintance.

MR. WEAYER reported, in connection with university selection, that the Rockefeller Foundation often received the very best, and the very worst, applications from the universities, those of the middle rank being frequently taken care of by university funds. He cited as a desirable practice that of the University of California, where university funds were used for the exploration of the projects set up by their own younger scholars, and the projects which have demonstrated their value are then referred to the foundations for support. He reverted to Mr. Crane's remarks on the costly but valuable method of gathering information practiced by the Social Science Research Council, and described the mass of information which is being continually collected and filed for the use of the Rockefeller Foundation. This information covers both enterprises and scholars, and is based upon confidential talks with scholars in all fields.

MR. ADAMS described the system in operation at the University of Illinois for grants-in-aid. According to their procedure, a committee on research, headed by the dean of the graduate school, is charged with the administration of the university's research funds, but it is also required that this committee pass on projects before any member of the faculty is permitted to request aid from the outside. This device is in some measure a protection against individual raids on funds that might be available for general assistance to research in the university.

In this connection, Mr. Frank asked whether there might not be some danger that new ideas in research methods and problems might fail of receiving the approval of such committees as Mr. Adams had described. William E. Lingelbach, Secretary of the American Philosophical Society, stressed the need of coordination between the agencies awarding grants-in-aid, and said that in his opinion other agencies should be permitted access to the confidential information gathered by the Rockefeller Foundation.¹ Mr. Bogert considered the selection of projects an easier task than that of personnel, and believed that a national organization should be competent to pass on the importance of projects submitted through central clearing committees. Henry Norris Russell, Professor of Astronomy, Princeton University, felt that as far as the American Philosophical Society was concerned, it had among its membership competent advisers in all fields, and, speaking for the Astronomical Society, he questioned whether it could give official advice. Mr. Leland, reporting for the American Council of Learned Societies, said that its committee had not encouraged official endorsements of projects by university councils and constituent societies.

The conference recessed at 12:30 P.M. for lunch.

Upon re-convening at 2:05, Mr. Leland introduced that part of the agenda dealing with the objects for which grants should be allocated, mentioning in particular the use of grants to take the place of salary, especially during the summer, in order to enable recipients in effect to purchase their own time,

and the use of grants for apparatus and consumable materials. Concerning the first, he reported on some of the vexatious refinements which may complicate an application made for the purpose of releasing the applicant's own time in order that he may devote it to his project. Materials account for a considerable part of the grants of the American Council of Learned Societies, but permanent equipment, such as books and apparatus, have been rarely purchased with the assistance of the Council's grants committee. In such cases as books, the committee has required the cooperation of college or university libraries, and in the case of equipment, title to that equipment has remained with the Council, and when applicants have concluded its use, it returns to the custody of the Council and is available for the use of other scholars. Mr. Conklin reported for the Philosophical Society that, in the early stages of its grants system, contributions had been made to pay the salaries of substitutes taking the places of grantees on leave of absence, but that this practice had been abandoned. He mentioned also in this connection a limited number of grants of an emergency nature to unemployed scholars. Mr. Swann inquired as to the practice of bodies represented in computing costs of travel and maintenance. He distinguished between making allowances for actual costs and providing for costs in excess of normal living expenses. He expressed himself as favoring the latter method. He considered the use of grants, for the purchase of exhaustible materials, as the most valid of the objectives mentioned, and referred to the difficulty, in connection with the purchase of apparatus, of deciding when the use of a piece of apparatus was actually concluded by the beneficiary of a grant. Conyers Read, Executive Secretary of the American Historical Association, questioned the usefulness of too minute an analysis of purposes for which grants may be expended, and called attention to the basic idea that the purpose of grants is to create conditions that will enable people to do good work. Mr. Bogert called the attention of the conference to the fact that in certain fields the question of the

patentability of the results of research is likely to arise Cyrus Adler, President of Dropsie College, urged that some study be made of research work done through commercial agencies, and adduced as examples the grants of the Radio Corporation of America and the research departments of banks and trust companies He considered that the selection of projects was inevitably a kind of gamble.

Turning to the sixth subject of the agenda, *viz* the range in size of grants-in-aid, Mr. Conklin said that in the experience of the American Philosophical Society the field of zoology was conspicuous for numerous applications of small size, but that the humanities and social sciences, especially archaeology, required grants of larger size, the average size of grants in all subjects has been \$1,500 In explaining the practice of the American Council of Learned Societies, Mr. Leland emphasized the Council's policy that grants are intended not to defray the total expenses of research undertakings, but rather to contribute toward those expenses It was reported by various representatives of research councils that the average grant of the National Research Council amounted to about \$600, of the Social Science Research Council to about \$450, and of the American Council of Learned Societies to about \$375. Mr. Weaver presented for the information of the conference some figures of the grants of the Rockefeller Foundation The average, he said, allocated by the New York office was about \$2,400, of the Paris office about \$1,175 He also showed the approximate percentage distribution of fellowships, grants-in-aid, and all other forms of support, in the fields of the natural sciences, the medical sciences, the social sciences, and the humanities, as follows:

	<i>Fellowships</i>	<i>Grants-in-aid</i>	<i>All other</i>
Natural sciences	18	13	69
Medical sciences	12	9	79
Social sciences	10	5	85
Humanities .	19	11	70

Mr. Leland, in opening the subject of continued support by means of grants-in-aid, distinguished between grants-in-aid to individuals and to projects. In the latter case, he

explained that the American Council of Learned Societies assumed a moral responsibility, but in dealing with individuals, the Council makes no commitment as to continued assistance to any enterprise

Forest R. Moulton, Permanent Secretary of the American Association for the Advancement of Science, expressed the need for definiteness in the contractual relation between an organization awarding grants and the recipients, whether individual or institutional. There should be no vague idea concerning the possibility of continuation, and no implied or explicit commitments. Mr. Compton, on the subject of continued grants, recommended that in dealing with institutions, a tapering off of assistance was advisable. Mr. Weaver compared the grants-in-aid to the light artillery or the air force in the attack upon ignorance. By this analogy, he stressed the mobility that is desirable. Mobility, in turn, precludes long-continued assistance. In no case should assistance in the form of grants-in-aid be continued for more than three years. Beyond that time, a grant-in-aid ceases to be such, and becomes a long-term program. Mr. Conklin reported for the Philosophical Society that its system precluded continuing commitments.

FRANK AYDELOTTE, President of Swarthmore College, mentioned the danger involved in continuing support, of creating a class of professional fellowshippers. Concerning reports, he advocated a minimum of schoolmastering, and questioned the need of periodic statements of progress.

Mr. Conklin next outlined the practice of the Philosophical Society with regard to reports of progress, which are expected from recipients of grants. These reports are frequently presented at the spring and autumn meetings of the Society, and may be available for publication in the Proceedings.

The question arose as to the frequency of reports, and particularly of the value of *ad interim* reports. Mr. Bogert's opinion was that the compulsion to stop and take account of work accomplished was of very real value to the recipients.

He therefore advocated periodical reports. Mr. Swann emphasized the value of a verbal presentation of final results, but questioned the use of periodical reports, because in many cases such reports required the recipient to say in rather elaborate language that he had nothing to show so far

It was Mr. Moulton's belief that it was much more important to make a careful investigation before allocating funds than to require reports afterwards. This attitude was also expressed by Mr. Weaver for the Rockefeller Foundation. Once a grant is made, the Foundation makes no formal requirement, although its officers are of course very glad to be informed of the progress of work. The practice of the Carnegie Corporation of New York as explained by its President, Mr. Frederick P. Keppel, was similar, but he described the system of the English Committee of the Carnegie Corporation as requiring more detailed and regular reports. Mr. Keppel reverted to the subject of continued support by grants-in-aid, and pointed out that such support may have the effect of taking a man out of the academic market, to his ultimate disadvantage. He therefore suggested that in all such cases arrangements should be made so that scholars should be granted leaves of absence during the period of their grants.

ALĚS HRDLIČKA of the Smithsonian Institution called attention to the need of professional advice as well as money in connection with the prosecution of research. He felt that when a program of research can win financial assistance from a foundation or society, it should also get the benefit of whatever expert opinion is available.

Mr. Conklin, in defense of the reports made to the Philosophical Society, pointed out the advantages to the individual accruing from the opportunity to present the results of his research to the Society, and mentioned as a not entirely irrelevant consideration the fact that the Society profited by having such reports for its meetings. John C. Merriam, President of the Carnegie Institution of Washington, related the place of reports in the program of the Philosophical Society to the query of Mr. Hrdlička concerning professional advice and

criticism. Mr. Compton inquired whether reports such as had been described were of interest to the foundations, and Mr. Weaver said they were, but that the great bulk of the information service of the Rockefeller Foundation was based upon informal reports and correspondence of the officers. Mr. Adams advocated reports as of value, particularly to the younger men, in training them in the presentation of results. Mr. Leland asked whether any of the National Councils required reports and if so what they do with them. Mr. Crane reported for the Social Science Research Council that no formal requirement was enforced by that body, but that correspondence with the recipients of grants was very active. Charles B. Lipman, Dean of the Graduate Division, University of California, briefly reviewed some of the preceding discussion, and concluded by advocating the smallest possible number of rules and the least possible amount of machinery in the administration of grants-in-aid.

Mr. Conklin prefaced adjournment by asking the members for an expression of opinion concerning the usefulness of such discussions as had been held. He indicated that if it seemed desirable to continue the discussion of the subject raised, or to exchange ideas on related subjects, the Philosophical Society would be prepared to act as host to another such group. It was the sense of the conference that opportunity should be given to exchange experiences in the administration of funds for the promotion of research, and that the next such opportunity should not be long deferred.

The conference adjourned at 4 30 P M.

THE RESPONSIBILITY OF ENDOWMENTS IN THE PROMOTION
OF KNOWLEDGE

FREDERICK P. KEPPEL

President of the Carnegie Corporation of New York

Lecture, February 19, 1937

Last month, Mr. Henry Moe of the Guggenheim Foundation and I were the guests of the Council of Learned Societies, an erudite gathering, I may say, something like the present one, only more so. We had been asked to speak upon a topic similar to that assigned to me tonight. But, deliberately, I fear, we misread our instructions and discoursed not upon what the foundation might do for the scholar, but what the scholar might do for the foundation.

I'm telling you this for two reasons: first, to remind you and to remind myself that your speaker has reached the stage where it is very hard for him not to repeat himself. He may succeed in changing his order and perhaps his emphasis, but he is not likely to tell you anything new. This is going to be particularly hard on my friends in the trusts and scholarly organizations, most of whom have heard me *ad nauseam* upon these matters.

My second reason is this: what I have been asked to discuss is in effect the relations between the people who are responsible for the distribution of endowment funds and those who by nature of their expert knowledge and their opportunity to apply that knowledge are responsible for the promotion of learning. And what I want you to keep in mind during this discussion is this: if this relationship is to be worth while, the lines of communication cannot be limited to a one-way track—the track from the scholar to the endowment. There must be a two-way track built, maintained and operated. Now if it is to be a real two-way track, there must

be some promotion of knowledge to make sure that the scholar understands the conditions under which these endowments have been created and the conditions under which they operate today

It is no new thing for human generosity to take the form of providing permanent support for some purpose dear to the heart of the donor. Even the foundation as a specialized form of generosity goes back at least to the days of Ptolemy the Great. The purposes for which endowments have been created and administered have, however, changed greatly in the recent past, and they are changing today. With rare exceptions our earlier English and American endowments were originally directed to either one of two purposes: to the immediate relief of suffering, of cold, or hunger, or pain, or to the spread of current educational opportunity—and remember all education was then religious education. We can trace the process by which these purposes have gradually changed from relief and routine to a search for the causes of human suffering on the one hand, and for the improvement of the educational process on the other. And we can see how these newer objectives, in turn, have in many instances been broadened to comprise scientific and scholarly inquiry in general.

We are perhaps too near the focus to see clearly as to the direction of further changes, but from the nature of my job I am perhaps in a position to see more straws than the average man and to observe their direction, and basing my judgment upon the number and direction of these straws, I should say that we are now entering a period of greatly increased interest in the spread of the new knowledge, of the fruits of recent research and discovery. I do not imply that research itself is to be neglected—far from it. This we should continue to do, but no longer to leave the other undone. This means, I hope, that the advancement and diffusion of knowledge will go hand in hand to a greater degree than they have in the past, or, if not actually hand in hand, at any rate, the lag between the two should be of much shorter duration.

In this country at least we still retain our almost mystical

faith in education, but we are beginning to realize that education is something that is itself ever-changing, that it is dynamic rather than static. The classroom remains the most obvious place for education to proceed, but not the only place; childhood and youth remain the obvious periods for education, but not the only periods. Now this process of the diffusion of knowledge and understanding lies at the heart of what we are coming to call adult education. It is interesting to recall that in the United States this term was almost literally unknown fifteen years ago

So much for the moment as to objectives. As to the operations of our present-day endowments, I am assuming that though endowment funds are spread widely through colleges and universities, museums, libraries and the like, more widely than most of us realize, what your President had in mind in proposing this topic was the independent endowment known as the foundation, and the foundation of comprehensive rather than narrowly prescribed charter. Now what must we bear in mind about the foundation of this character so far as the advancement of knowledge is concerned? In the first place, let us understand that in the aggregate the financial contribution from this source will always be a relatively minor contribution. Not only has the foundation itself other responsibilities, but the amounts available for the purpose from other sources, taxation, individual gifts, existing institutional endowment, legitimate earnings, such as student fees, and in many fields the contributions of industry—all these will at any time and for any purpose greatly exceed the sums which it is possible for any single foundation, or indeed for them all, to contribute

Though strictly limited in its scope, the foundation is nevertheless a factor of the first importance, for it has certain great assets. It is free to choose its objective, it can give when others withhold, it can give quickly, and if it keeps its funds free from obligations against future income, it can continue to give. Foundation support for any enterprise should be significant for its timeliness rather than for its

amount, it should reveal imagination and courage. Incidentally, it needs nearly as much imagination and more courage for a foundation to stop support when the area of diminishing returns is reached. But only by so doing, can it continue to be creatively useful.

Let us remember also that, not everywhere or always, but very generally today, the foundation realizes that money is and must be kept a secondary factor. The men and women concerned with foundation policies and administration have to talk in terms of money, for after all books must be balanced and promises met, but deep down they realize that the life is more than meat and the body than raiment. Bear in mind also that the foundation of today, generally speaking, is no longer satisfied merely to adopt a defensive attitude toward the proposals which may come to it, it itself endeavors to take the initiative.

These are some of the things which the scholar must know if he is to work to good effect with the foundation, and there are certain others. He must understand that in any foundation the final power of decision rests with a lay board. Individual members of this board may be distinguished professionals in various fields, but for practically every question coming before the board as a whole the vote of each member is of necessity a layman's vote. This state of affairs is of course quite characteristic of our Anglo-Saxon tradition, for it obtains not only in foundations, but also in colleges and universities, in libraries, museums and hospitals.

Now these laymen do not themselves administer the trust, or perhaps I had better say that when they try to do so everybody gets into trouble. To prepare the material upon which it must act, and to carry out its directions, the board appoints a staff composed of persons (like me, for example) who may perhaps be most kindly described as semi-professional in character. Such persons comprise today a minor subcaste in American life and are sometimes known as philanthropoids. Now how does the philanthropoid go about his business? This is like asking, "How doth the little busy bee

improve each shining hour?" Of course, like any other white collar worker, he must keep records and accounts answer letters, receive visitors, but he must manage to save sufficient time for his peculiar and, to my mind, his primary task. If the lay board for which he works is to have an adequate basis for its decisions upon the subjects before it, he must gather his honey in the form of expert and professional information and recommendation from the people who know. And I may add that of all foundation activities, it is precisely in the fields we are discussing today—the fields of scholarly inquiry—that the trustees and the semi-professional executive are most likely to go astray, unless they seek and find the very best expert help available

I can't go into all the different ways by which this may be accomplished—the building up of a professional full-time staff within the foundation organization, the engagement of experts on a part-time basis, permanent or temporary, the formation of *ad hoc* advisory committees—these schemes and others in which the foundation selects its own advisers have all been tried and are still in operation in one foundation or another. It seems to me, however, that there is today a movement away from selecting our own advisers upon scholarly questions and in the direction of turning to the existing groupings of scholars for counsel. The development of the three great representative Councils, National Research, Social Science, and Learned Societies, has undoubtedly stimulated this trend. For one thing, it is for obvious reasons desirable that the advice which comes upon delicate matters of selection should be anonymous so far as the foundation itself is concerned, and the existence of the scholarly middleman makes this anonymity much less difficult to achieve.

If we in the foundations look back from our side of the line or if the scholars look back from their side, neither can, I think, be wholly satisfied as to the results of our cooperation thus far, but this is as might be expected, for it is a new game for both sides. As we learn more about the game, we should both play it better in the future.

My own belief, and remember it is just one man's belief, is that the American foundation today is characterized by humility of mind rather than by complacency. The foundation recognizes both the responsibility placed upon it and the need of help in order to exercise that responsibility. It does not regard consistency as a virtue in itself. The foundation looks for its broad results to variety rather than to uniformity, to an informal rather than a formal method of approach.

Let me bring one more point to your attention. We are likely to think of the foundation solely as a distributor of funds to individuals or to organizations, forgetting that not a few foundations, including some of the most important, are themselves operating agencies. The Carnegie Institution of Washington and the Rockefeller Institute for Medical Research have from the first been of this character, and it is, I think, fair to group with them such more specialized endowed organizations as the Oceanographic Institute, the Huntington Library, and Mr Andrew Mellon's recently created Trust. In addition, certain trusts of more general character, like the Commonwealth Fund and the Carnegie Endowment for International Peace, have as a matter of policy become operating agencies, since their trustees have decided that they can best fulfill their obligations to their donor by so doing. And may I add in this presence that the American Philosophical Society, through the receipt of Dr Penrose's great bequest, has after a long and distinguished career of honorable penury been, so to speak, born an operating foundation out of due time.

Thus far this has all been pretty general in character, but before I sit down I should like to be more specific, and as a basis for this specificity, let me recall briefly some of the things I have said, perhaps interpolating a little as I go along. First, that without neglecting the increase of knowledge through the support of research, the foundations to an increasing degree are becoming interested in the diffusion of knowledge, and that this is in the interest alike of the individual and of society, that, after formal training is over, the

educational process is none the worse for being disguised as recreation—as a hobby or a sport. At this stage, also, understanding is more important than additional facts, once enough facts have been mastered to furnish a basis for understanding. Second, that the foundations are coming to realize that their usefulness in all these matters depends upon the establishment and maintenance of a two-way track between the foundation and the scholar. Finally, that, while in general the foundation does not itself administer the funds which its endowment provides, there is excellent precedent for its doing so in specific cases

Much is already being done along the lines of non-professional adult education, in music and the drama, in the pictorial arts, in current affairs, particularly economics and international relations, and also in other fields, as in the case of the parent education movement

There is, however, a broad range of human interest where adult education is lagging behind, and it is to this that I wish particularly to call your attention tonight. I think it can be legitimately included in the subject assigned to me, since it might be made an excellent example of a fruitful relationship between the scholar and the foundation, and, further, and this is of course the real reason, it's a matter which I personally have very much at heart. Here in Philadelphia, I may say it is a matter upon which I have a 'concern.'

In a civilization like our own about the last place where one would look for this unsatisfactory situation is in the field of science, and yet it is precisely in this field of science that we have made the least progress in our adult education.

Science is, of course, a broad and inclusive term, and here and there we find exceptions to our generalization. In astronomy and in American archaeology, for example, though the number of amateur students is not large, much first-rate work is being done by them. Agriculture and particularly horticulture—the amateur farmers and the amateur gardeners who are also students—represent a much larger if not perhaps so distinguished a participation. Generally speaking, how-

ever, science is a neglected field. In a civilization based to a degree unimaginable in the past upon the applications of science, we find the classroom opportunities for the study of science by adults, through university extension and the like, to be today less than 6 per cent of the total offering. (I find this percentage in Dr. Benjamin A. Gruenberg's interesting work, *Science and the Public Mind*.) In the less formal opportunities for adults, such as those offered by libraries and museums, it would be much harder to estimate the proportion to be credited to science, but I fear no one familiar with the facts could give science other than a low relative position.

Suppose we should set our minds to increasing the proportional opportunities for adults in science, what have we to build upon? Well, we have these factors. For one thing, in practically every field the American scholars in science are no longer followers, but leaders. For another, our people as a whole have reached a level of education, none too thorough, perhaps, but, nevertheless, a level not approached anywhere else in the world. The Office of Education at Washington estimates that there are approximately two and a half million living graduates of colleges and universities in the United States. Of these 40 per cent are below thirty years of age, and 70 per cent below forty. It also estimates that there are living today more than fourteen million graduates of high schools. It is rather interesting to note that in the case of high school graduates the proportion of boys to girls is about 4 to 5 and that the proportion of men to women among college graduates is about 9 to 5.

In every high school a considerable degree of science is prescribed, and in every college some is prescribed and a very much larger amount elected. Beyond this, our adult population contains substantial numbers of men and women, engineers, chemists, doctors, dentists, nurses, for example, who in addition to their preliminary education have received a substantial degree of professional training in science.

In our universities, museums, parks and gardens, libraries,

institutes and laboratories, there is today available scientific equipment, collections of material, books and journals, which represent great wealth, even when measured by the imperfect scale of dollars and cents. And we must not overlook the corresponding material which is in the hands of individuals or corporations, much of which is or might be made available. Funds exist today for keeping this material up to date, for its growth and its service.

A very few years ago no one would have thought it worth while to include in our list of potential assets the fact that in the United States the spirit of intellectual inquiry is free. That would have been taken for granted. But today our relative freedom, despite Scopes Trials and teachers' oaths, must be reckoned as a very precious asset. If we look overseas, certain countries which have made great contributions to the advancement of learning in the past appear to us to be in the process of committing mental suicide. This is, let us hope, an appearance and not a reality, but at the best they seem to be in for a considerable period of intellectual hibernation.

I have spoken of our potential assets. Let me say a word about our actual liabilities. The first I should mention is a disability affecting a full half of our population. I refer to a curious shyness on the part of our males about being caught at improving themselves culturally. Adult education in the fine arts, for example, has in recent years shown a striking growth, but until very recently it looked as if this interest must represent what the geneticists would call a sex-limited character.

Another liability is the traditional attitude of so many men of science, the very men who should be the leaders, not only in the advancement but in the diffusion of knowledge. It would be too much to say that they regard themselves as the High Priests of Mysteries in which the *vulgus profanum* has no place, though this cruel thought does sometimes come to one's mind. It would not, however, be unfair to say that most of those who are themselves advancing the frontiers of scientific knowledge are frankly not interested in the popular

diffusion of such knowledge. When approached upon the subject, they are likely to reveal a fear that if it were known by their scientific colleagues that they were developing such an interest, they would lose face, and this despite excellent examples to the contrary to be found in England and elsewhere.

Certain other leaders point out that the unevenness of preparation in any adult group adds enormously to the difficulties of laying any solid foundation of fact upon which a structure of worth while understanding can be erected by the individual. This liability deserves serious consideration. If it is proposed merely to carry over the classroom techniques based upon uniformity of previous preparation, one can well understand the doubts and fears of these leaders. We do know, however, that excellent results are actually being obtained when instruction is individualized, and more important, when the adviser has skillfully limited the student's own objective to a degree of understanding which his factual structure can safely carry.

Even when the leaders in science are willing to talk to the laymen about these matters, it often develops that the two groups are not talking about the same thing. What the scientist has in mind is a broader spread throughout the American people of a belief in the importance of science and of the scientific method in modern life. Now this is admittedly most desirable. Indeed it is hardly reasonable to expect that in the long run funds will be forthcoming for the support of scientific research in adequate amount from taxation and corporate or private sources, unless there is developed a more general understanding of the objectives of science on the part of the public.

But surely this is not the whole story. Hasn't the individual American adult a right not merely to worship, but to learn, and in learning will he not only enrich his own life, but help the course of public appreciation in the most effective possible way?

Now remember, I am ready to admit that something is already being done for the adult of inquiring mind in libraries,

museums and the like, even in colleges and universities. I say even, because these institutions have thus far interested themselves almost exclusively in the adult who has a vocational rather than cultural incentive for further study—a wholly worthy purpose, but not the one we are discussing tonight. My complaint is that not enough is being done, and certainly not enough opportunity is given for a participating activity on the part of the student, through laboratory facilities and the like

Before we can fairly say that there is anything that can be called a serious movement, many first-rate men and women must set to work to organize the material best adapted to the interests and capacities of the adult non-expert. Incidentally, such persons will find out for themselves that the job will involve an internal reorganization not only of their habits of thought, but of their use of the English language as well, and this, as I have intimated, will mean considerable shaking loose of traditional adhesions. Institutions must open their doors, and in particular more colleges and high schools must throw open their laboratories and study collections. For use in communities where it is not now available, we must have suitable science material "on the road" just as we have our traveling exhibitions of pictures and our traveling orchestras.

I have tried to be fair in setting our assets and our liabilities against one another. Certainly I have tried not to underestimate the liabilities. Do you agree with me that all things considered, the assets outweigh the liabilities? I hope you do. Well, if wise people like ourselves agree that something ought to happen as to science and adult education which isn't happening today—at least not happening to any satisfactory degree—what is the matter? Is there anything we lack? I think there is.

First, there is the question of money, secondary, as I have said, but still not to be overlooked entirely. Ten years ago in the intellectual climate which then prevailed, if we had been thinking of stimulating adult education in science, we should probably have set ourselves to work out an elaborate

pre-budgeted plan, involving perhaps hundreds of thousands of dollars, in which we would have tried to anticipate all the details of administration and operation. Today, thanks largely to the depression, we are in a more chastened spirit. We are ready to start simply and modestly, and to move forward step by step. We frankly don't know today just how the cat is going to jump. Let me give you just one example of what happens when a man tries to outguess the future. You all know that Benjamin Franklin bequeathed to the cities of Philadelphia and Boston a thousand pounds each to snow-ball for a hundred years, the accumulation at compound interest to be used for some needed public purpose. But do you remember the purposes he suggested in his will? The wisest man of his generation failed to foresee that a public water supply and sidewalks would have been provided long years before his bequest could be available.

If the idea itself is sound and if the right people are dedicated to its development, a relatively modest sum would be sufficient to set things going. Should things go well, the ultimate expenditures would probably be greater than under any pre-budgeted scheme, but the money would be more wisely spent. Where would the money come from? In part doubtless from foundations, certainly at the outset, in part also from student-fees, from public moneys, and from individuals and groups interested in local developments. Judging by recent experience in other fields, some would be found, perhaps a great deal would be found, in the debatable land lying between philanthropy and business.

But there is something much more important than money which is lacking today. We need most of all a focus, a central agency which has a reputation to lose, for such a reputation offers the best, perhaps the only, security for investments of this character. I mean a reputation for public spirit, for intellectual honesty, and in this particular case for high scientific standards as well. To such a body could safely be entrusted the staff-work of the enterprise, the establishment of relations between the leaders in science and the agencies of

adult education. Where the publication of simple but authoritative material is needed, as it certainly is needed in many branches of science, such an agency could stimulate its production. All along the line it would soon become the general clearing house for ideas

Let us for the moment forget the word Science, and let us remember the term which Benjamin Franklin used and his followers used for nearly a century—Natural Philosophy. And then let me very respectfully suggest that, if it so desired, the American Philosophical Society might become just such a guiding agency. Was not the Society founded largely for this very purpose, and has it not had a long and honorable tradition in the diffusion of scientific knowledge and understanding? Is it not today an operating foundation? I make the suggestion in all seriousness, but please understand that I am not proposing that the American Philosophical Society should, in the current phrase, be left with the bag. Other agencies must help, local and regional, national, perhaps international. They must help both with money and in service, but far more than money and far more than scattered service, we need a focus, we need leadership.

Open Session, February 20, 1937

**THE MOST IMPORTANT METHODS OF PROMOTING RESEARCH
AS SEEN BY RESEARCH FOUNDATIONS AND INSTITUTIONS
JOHN C MERRIAM**

President of the Carnegie Institution of Washington

Research by purpose and definition of the term aims at such a wide variety of objectives and takes such different and irregular paths that it is difficult to segregate any small group of methods as clearly the most important. And yet it is desirable to consider some of the means by which creative activity or the advancement of knowledge may be aided.

If one were to select from the many types of effort developed for promoting research, the classification would presumably include methods on the one hand expressed in terms of financial aid and, in another direction, by efforts to stimulate interest in research and develop activities leading to creative work. There would be, further, methods developing out of the interests of widely differing institutions and activities in which the research promoted would be only the means to an end, and the type of promotion used would depend in some measure on the ultimate objective, as in the industries.

The classification of agencies listed in the program of this meeting is itself an indication of the various methods of approach to the problem, different means by which investigational activities may be promoted, different means of interpretation, and different objectives. While learned societies and academies are concerned with many objectives which are the same as those of the university and the research foundation, there may be a considerable difference in the fundamental objective and the purpose for application of the results. It is to be expected that these differences will express themselves in the methods used for promotion of research.

If additions were made to the list I would expect to include reference to so-called professional activities represented by the practice of medicine and health protection, together with agriculture and those industries based upon the physical sciences. While the specific objective of all these activities is professional in the sense of service applied for purposes in which compensation is involved, we must recognize the fact that great contributions to knowledge arise through all of these types of work, and that some aspects of research thrive especially well in relation to activities which involve the application principle. The promotion of research under the conditions presented by great industries offers some of the most interesting suggestions and presents many points which may well be considered in discussion of the investigation problem in other fields.

It is, I believe, important to say that contrary to what seems to be a widely-held opinion, the securing and organization of funds does not necessarily constitute the thing of greatest importance in the advancement of research. I am convinced that in many institutions there is not only adequate talent but with this abundant material which might be used, without support of large funds, for constructive study which would be of great benefit to mankind, and would be tremendously important for the individuals concerned.

There are of course many phases of research in which advance of knowledge requires use of extremely valuable materials, the construction of expensive apparatus, or the costly work of gathering data over a wide area or a long period, and therefore special funds must be available if a really important work is to be accomplished, but the problems of this type constitute only a small part of all that needs to be done for the advance, organization, and application of knowledge. I have known a dentist in a small town rather remote from centers of education and research to build up not only an interest but an enthusiasm for a study of nature

and for real advances in research by attracting the interest of teachers in the high school, and this extended to the students, the people of the community, and to major institutions of the State.

The phase of the subject of finance which has perhaps been discussed most in recent years relates to what is commonly known as the grant-in-aid, which is also commonly a grant to an individual. Closely involved with the grant-in-aid question and the allotment of funds to an individual, there is of course the seemingly different point of view concerning selection of an individual because of his interest and ability, or the selection of a problem by reason of its importance.

The stress placed on the idea of selecting the exceptional man by Mr. Carnegie has extended itself in various ways and has been interpreted differently by institutions in their efforts to promote research. It is interesting that there has been less notice of the corresponding stress laid by Mr. Carnegie on the idea of giving support to special projects such as characterized a part of his giving. In the third of the major gifts to the Carnegie Institution by Mr. Carnegie, the special point mentioned was the support of the large project at Mount Wilson Observatory, which was set forth in an interesting form through Mr. Carnegie's statement that he desired to have the work at Mount Wilson pushed as he desired to repay to the old land some part of the debt which we owe by revealing more clearly than ever the new heavens.

The administration of grants-in-aid has been tested out by a great number of experiments and experiences, so that any institution entering upon consideration of this method of promotion of research should now find it comparatively easy to learn the opportunities and at the same time the dangers of this means of advancing investigation. If the assistance is given to a man of exceptional ability in certain directions, it will be recognized that the aid is not assured alone in terms of money, but it must include those elements which have to do with the furtherance of research, including the

mechanism by which investigation is conducted, the environment in which the research is carried on, the opportunity for exchange of ideas on the project, and the means for recording and interpreting the results

If the grant is directed toward the solution of a particular problem, it is essential that attention be given also to the discovery of individuals having such interest in the project that, whatever the importance of the subject its investigation may receive such attention as is necessary if there is to be advance and better organization of knowledge.

Although myself dedicated to service in the field of research, I have consistently maintained the position that real advance of research depends upon having a clear idea as to the general purposes of investigational and creative work. I believe also that real attainment depends upon maintaining a clear picture of the relations between research and other aspects of science and human interest.

It would be easy to overdo the discussion of purposes of research in terms of broad generalities, perhaps neglecting that intensive study upon which the gathering of facts and the advance of knowledge depends. On the other hand, it would be equally unfortunate if multitudes of investigators in widely separated fields were to delve into the deeper and darker recesses of the universe of things and of thought only to pile up stone and bricks without knowing either the broad structure of the formations from which they are taken, or the ways by which the materials secured can be built into a new type of structure.

Just as a means of promoting research, it would be important to make certain that the scientific and cultural background of the investigation be of such nature that we shall not only place the new facts where they are most effective, but that we shall have vision of the relation between the elements involved as the work proceeds. Research is not solely digging for facts; it is frequently in large measure the imaginative treatment of ideas and materials with a view to discovering relationships which we have not been able to understand.

WARREN WEAVER

Director for the Natural Sciences, Rockefeller Foundation

Mr. Weaver's extemporaneous remarks on Saturday morning amplified the following points:

(1) However much philosophy may underlie a grant-in-aid program, however many regulations may exist, the matter finds its practical focus in the ultimate answer of yes or no to a definite request for funds. That, the primary business of a financial distributing agency in the field of promotion of research is to give money to the right man and the right project rather than to the wrong man and the wrong project.

(2) The phrase "the right man and the right project" is not strictly proper. One ought rather to say "the better man and the better project" for the word "right," at least in this connection, has meaning only in terms of the alternatives.

(3) But if decision can be made only in terms of alternatives, then clearly a knowledge of alternatives is essential.

(4) Are alternatives sufficiently and satisfactorily represented in the group of other applications which will automatically arise in response to a public notice? The speaker thinks that this will seldom be true and may not safely be assumed. In particular, those persuasive scientific mendicants who may be briefly characterized as "good askers" will appear frequently. They have the contacts, the information, and the techniques which give them an undeserved advantage over the shy, the modest, the obscure, the poorly informed, and the relatively isolated worker.

(5) It is therefore suggested that any organization distributing such funds has a measure of responsibility for informing itself concerning men and problems. Since this seldom can effectively be done, for very wide geographical areas or for very wide fields of subject matter, by any one organiza-

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tion, it is suggested that these considerations lead rather definitely to the suggestion that a grant-in-aid program will be more wisely administered if it is restricted to certain definite areas. Such restriction would have an unhappy and undesirable effect upon the general advance of science, were it not for the fact that the naturally varied interests of different groups will almost inevitably lead them to adopt different areas for concentration. Universities, as custodians of general knowledge, are responsible for maintaining a rounded and complete program. Certain other organizations, however, have the freedom and opportunity, and perhaps also the duty, to be selective.

**METHODS OF PROMOTING RESEARCH, FROM THE POINT OF VIEW
OF SOCIETIES, ACADEMIES, AND COUNCILS****WALDO G. LELAND****Permanent Secretary of the American Council of Learned
Societies**

It has been said that every American scholar has two allegiances, one to his university and the other to the learned or scientific society devoted to his special field of study. American scholarship is strongly organized in national societies or associations, many of which are now of more than fifty years standing

Each of these societies is composed of the American scholars in some field of study, as chemistry, geology, mathematics, history, philology, oriental studies, etc. Their membership ranges from a few hundred to many thousand, and their resources from barely enough to maintain existence to substantial funds. Practically all the societies hold annual meetings, which are events of considerable importance, and most of them support at least one periodical, some of them devote much attention to the pedagogy of their subjects; some endeavor to prepare important tools of research, some set up projects of research and try to carry them through; numerous societies are interested in presenting their subject matter to the public, and take some part in adult education, through such devices as popular publications or radio talks, or by admitting to their membership laymen who are interested in their fields. In this way many societies have in their own ranks an elite part of their general public.

In addition to the societies or associations, there are three organizations of national scope that closely resemble the traditional European academy. In order of foundation these are the American Philosophical Society, the American

Academy of Arts and Sciences, and the National Academy of Sciences. The last of these is restricted to the sciences, but the other two include all the fields of knowledge. These are of select and restricted membership, which tends to be somewhat regional and to represent the middle and upper age levels of scholarship. They hold stated meetings at regular intervals, issue publications, award prizes, and assist research by means of grants

It is pertinent now to enquire in what ways such organizations as those just described can best promote research

In the first place, it is evident that their meetings afford the best opportunities for scholars in the same field, or, in the case of academies, in different fields, to come together to discuss their problems, compare their experiences, and to consult as to desiderata. These meetings, with the opportunities they offer for useful and stimulating contacts, are an important factor in the environment of scholarship, and, indirectly, in the promotion of research.

In the second place, the periodical or other publications supported by the societies are the principal media for the communication of the results of research, the exchange of ideas, and the appraisal and criticism of work accomplished

Finally, the societies furnish the occasion and opportunity for much planning of research, and they may, if resources permit, serve as agencies for conducting investigations.

The COUNCIL, as we know it in America—and it is essentially an American product, was the outcome of conditions created by the Great War. The necessity for coördinating the activities of many agencies, of enlisting the coöperation, on a national scale, of many different competencies, of planning rapidly and accurately measures designed to meet the emergency, led to the organization of the National Defense Council and of its coadjutor, the National Research Council, the latter being created under the charter of the National Academy of Sciences. At the same time, the National Council on Education was organized for the purpose of mobilizing all the resources of the institutions of higher

learning. These two councils, born of war conditions and necessities, survived the emergency and, adapting themselves to more normal conditions, were found to be agencies capable of rendering many useful services. The American Council of Learned Societies, organized immediately after the War, was intended to be the counterpart of the National Research Council, serving for the humanities and the social sciences in much the same manner as that organization served for the natural, physical, biological, and exact sciences. A little later, the organization of the Social Science Research Council supplemented the Council of Learned Societies and took over its activities so far as the fields of the social sciences were concerned. The set-up was thus complete, with four major councils functioning on a national scale in the fields of education, the sciences, the humanities, and the social sciences.

The activities of the last three councils,—that is, the subject-matter councils, have been fundamentally similar, although showing many differences in detail and in operation. Each, however, has had as its chief objective the advancement of those fields of knowledge that fall within its scope. Furthermore, they are similar as to organization in that each is a federative body composed of representatives of its constituent societies and associations, which last include practically all American scholars active in the disciplines to which they are devoted.

The councils have in no way supplanted the societies or associations, but they have become agencies through which the latter can achieve objectives of mutual interest, can coördinate their activities, and can join forces in planning for the promotion of their interests.

The recognition by foundations and other benefactors of the councils as convenient and reliable agencies for undertaking activities that they are disposed to encourage or assist, and also as sources of useful information and advice, has made it possible for the councils to attain to positions of influence and responsibility in their respective domains. Thus they have administered funds for fellowships and the

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training of research personnel, for assistance to the individual scholar by means of grants-in-aid, for assistance to the publication of meritorious works, for the planning of activities and undertakings important to the advancement of scholarship, and for the organization and execution of large-scale coöperative enterprises of research. All these activities are designed to encourage and promote research and to advance knowledge. What special advantages or facilities do the councils have for carrying them on?

It is obvious that, in the first place, they have the advantage of being representative bodies and of being able to draw upon the resources of ability possessed by practically all the scholars in their respective areas. In this, they differ from the universities and from the academies of select membership. In the second place, they include all the disciplines or specialties within their general areas, and in this they differ from the societies or associations that are devoted to special fields. It seems clear, therefore, that the councils' activities should be chiefly such as they can perform more effectively than the university, the academy, or the society or association.

Remembering that the individual council is devoted to an important segment of knowledge, but not to the entire circle, it can endeavor to develop within that segment a sense of the community of interest of the disciplines that compose it. It can render conspicuous service in breaking down barriers between disciplines and in making possible contacts on a large scale between scholars of different, though potentially related, fields. The effect of this action upon the promotion of research is to encourage new points of view, to develop new methods of investigation, and to suggest new implications and applications of knowledge.

The council can also take a leading part in the promotion of fields of study that are relatively neglected. An example of this activity is to be found in the development of Far Eastern—especially Chinese—studies during the last eight years by the Council of Learned Societies, a development which has resulted in enlarging the scope of American human-

istic scholarship to include a field that affords unlimited opportunity for new research of especial importance to the world at the present time.

In activities of planning, the council derives a special advantage from its representative character and from the broad base on which it rests. It is almost the ideal agency for appraising the needs of its segment of scholarship in terms of tools of research, and for directing and coordinating the production of those tools. Such implements as inventories of materials for research, bibliographies, corpora, dictionaries, etc., can best be produced by the collaboration of many workers, usually drawn from different fields, laboring under a unified direction.

The council can also take an effective part in planning large scale cooperative enterprises of constructive research, which require collaboration of scholars from different disciplines. Whether the council can as successfully set up and execute these different enterprises depends on circumstances. The success of the Council of Learned Societies in carrying through the *Dictionary of American Biography*, and its excellent progress with the *Linguistic Atlas*, indicates that under favorable circumstances it can serve as an operating agency, but, in the absence of such circumstances, it seems likely that the effective operation of projects of research can best be assured by an institution, such as the university or institute of research, where definite conditions of employment, control, and responsibility exist.

The advantages of the council over the university or academy or society in administering assistance to the research of the individual scholar are of degree rather than of kind. The assistance administered by the council is broadly distributed. It is not restricted to a single discipline, nor to the members of a single group, the actual awards are made by scholars who, usually, are not the associates or colleagues or even the personal friends of the applicants. What may be lost in intimate knowledge of qualifications and merits is compensated by a greater degree of impersonal objectivity,

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perhaps also by a somewhat broader outlook over the entire area of the council's interests.

The councils have also rendered important services in the administration of the post-doctoral research fellowships provided by the Rockefeller Foundation, and two of them (the Council of Learned Societies and the Social Science Research Council) are experimenting with fellowships at the graduate-school level for the purpose of improving research personnel in their respective areas.

The two councils just named have given much attention, through a joint committee, to the development of new, rapid, and inexpensive methods of reproducing materials for research and of publication, and the results of this committee's activities are already beginning to have an important influence upon conditions of research, and upon facilities for publishing its results.

By way of summary, it may be said that the societies, academies, and their federations the councils, are important agencies for promoting research, but that such promotion is most effectively accomplished through making possible regular contacts among scholars, by supporting learned and scientific journals and other scholarly publications, by breaking down barriers between disciplines and by developing new fields of study, by estimating the needs of scholarship, especially in terms of implements and tools, and by planning cooperative undertakings.

THE SUPPORT OF RESEARCH IN THE UNIVERSITIES

ALEXANDER G. RUTHVEN

President of the University of Michigan

Among the points raised in the conference, the difficulty of separating men and projects in analyzing requests for grants-in-aid was frequently stressed. It seemed to be clear that both must be considered, but little was said directly of the necessity of a knowledge of the institutions, including an appreciation of the trends in education, in appraising the significance of proposed research programs. The institution as the environment is as important as the investigator and his problem, and the trends of institutional development are bound to influence the effectiveness of the foundations in stimulating research and in increasing knowledge.

There appeared to be rather general agreement that the support of scholarships and fellowships yields, on the whole, good results, while the so-called grants-in-aid are the most difficult to administer, if not the least satisfactory method of assisting investigation. There are four conspicuous difficulties attending the latter form of aid. The grantee is very prone to interpret the assistance given him as a contribution to a project and to lose sight of time limitations, frequently to his own chagrin as well as to the discomfiture of his institution and the embarrassment of the grantor. Again, it is often difficult to predict very accurately the results to be obtained from a particular combination of investigator, problem, and institution, so that even able investigators occasionally fail to bring their studies to proper fruition because of environmental conditions and relations which were not foreseen. Further, grants are sometimes made for investigations outside the fields of knowledge cultivated by particular institutions, and which, because of the demands

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which they make, interfere with general research programs. Finally, as is well attested by experience, investigators exhibit great differences in ability to "sell" their projects, and, since proficiency in salesmanship is quite unrelated to ability in research even the product of well advertised investigations may be disappointing.

In view of the uncertainties which beset grant-in-aid programs and the profound changes to be made in education in the near future as a consequence of the growing competition between the institutions of higher learning, the methods to be adopted by foundations would seem to be manifest at least in one sector of their field of interest. The increase of knowledge can best be promoted in the colleges and universities, first, by cooperation between the foundations, the councils, and the institutions in an attempt to organize a national program of research, involving a regional distribution of activities, second, by increasing the number of scholarships and fellowships—these to be awarded only upon the recommendation of the school in which studies are to be pursued; and, third, by discarding the grant-in-aid in favor of the project-grant in the form of period allotments or endowments. This general method of promoting research in the universities will not only insure more uniform results than can be expected by the grant-in-aid but, what is equally important, it will contribute to the important task of building an integrated system of higher education which must now appear, not as the result of regimentation but as a product of intelligent leadership, if the increase and dissemination of knowledge are to go forward satisfactorily.

THE SUPPORT OF RESEARCH IN THE UNIVERSITIES

EDWARD P. CHEYNEY

University of Pennsylvania

Mr Cheyney spoke of his experience as chairman of a Faculty Committee on Research Grants which has been in existence for six years. It was appointed in the belief that universities as well as endowed foundations and industrial concerns should be active in the work of research. It has been given some \$80,000, spread over several years by one of the great foundations and has received small annual appropriations from the University.

Its object has been to create an interest in research among members of the Faculty, rather than to obtain the results of the research, though these of course accompany the main object. Its grants have therefore been small and numerous, 340 grants having been made in the six years of an average amount of \$275. The object desired has been largely attained, interest in research having been widely disseminated among members of the Faculty and the quality of teaching improved.

The difficulties met have been especially three. We have been constantly told by applicants for grants that what they need most is time not money. This brings up the question whether men engaged in the work of teaching can at the same time do research, and whether it is a proper function of a university to expect or encourage research among its professors. Both of these questions should be answered in the affirmative, the advantages are so great that a struggle must be made to overcome the disadvantages.

Secondly, avenues of publication have proved as necessary as aid to carry out projects of research. But this is rapidly being overcome by endowed means of publication. Moreover, the research worker must learn to put his results in such a form that they can secure dissemination. It is not necessary

that the results of every piece of research should appear in the form of a book.

Thirdly, applications for aid have proved to be much more numerous in the physical and biological sciences than in the humanities and the social sciences. This is unfortunate. One of the greatest needs of our time is undoubtedly for research in the social sciences. Political, economic and social maladjustments are threatening the very life of society and it is only to the results of research in these fields that we can look for safety. It is noticeable also that business is more and more asking to have research made and is coming to the college professors to make it, as being the only trained and at the same time independent investigators. Perhaps the separate departments of industrial research are fulfilling this need, but why so few demands on the funds are made by individual professors in this field is a problem that needs investigation.

**REPORT OF THE COMMITTEE ON RESEARCH,
APRIL 1936-APRIL 1937**

EDWIN G. CONKLIN

Chairman

This report covers the period since the last Annual Meeting of the Society and is in continuation of the report given one year ago, which was published in the *Proceedings*, Vol 76, No. 3, June, 1936

The membership of the Committee during the past year has consisted of William F Albright, Isaiah Bowman, Edwin G. Conklin (Chairman), William E Lingelbach, John A Miller, Roland S. Morris, Alfred N Richards, W F. G Swann and Hugh S. Taylor. Owing to Dr. Taylor's absence from this country during the second half of the academic year Dr. Harold C. Urey was appointed to serve in his place. Thus it will be seen that all four Classes of Membership in the Society and nine different subjects are represented on this Committee.

The Committee has held five regular meetings during the year, namely on June 2, October 7, December 11, 1936, and February 12 and April 9, 1937. The rule was established that applications for grants must be sent in at least ten days before the first of the months in which meetings are held in order to enable the executive office to multigraph the applications and supporting letters and to distribute these to all members of the Committee well in advance of the meeting, and also to permit members of the Committee to consult with applicants or others who are experts in the field of the research proposed. In order to diminish the labor of this multigraphing and also to secure in brief form the detailed information desired blank forms of application and of letters of recommendation have been used; these letters must come directly

to the Committee and not through the applicant, but it is optional with the applicant whether or not he will ask others to send in supporting letters.

The members of the Committee have taken their duties seriously and if it has been necessary for any one of them to be absent from a meeting, he has generally submitted in writing his opinions of the various applications which were being considered. In addition members of the Committee have investigated many of the applications either by personal interviews or correspondence with the applicants or others whose opinions were desired. This has involved a good deal of work for the Committee as well as for those consulted; and as Chairman of the Committee I wish to thank all those who have given freely of their time and services in this important field of the Society's work.

During the year the Committee has received and considered 115 applications for a total sum of \$226,384.07. Of these 54 were approved for a total sum of \$55,332.00 or an average for each grant of \$1,025, while 58 were declined and action on 3 was deferred. Many of those declined were well worthy of support, but it was necessary to reduce the sums asked for in many instances and to decline others altogether.

In the report of last year all the grants made by the Committee since its organization in 1933 were listed numerically in the order of their approval. There were 98 of these grants for a total sum of \$149,750 or an average of about \$1,500 for each grant. The grants made during the past year, listed numerically in the order of approval and acceptance follows:

1936, June 2

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| Grant No 99—J W Beams, University of Virginia, for the study of the nature of lightning. Photography of lightning discharges and measurement of electrical polarity and electrical moment of the flash. Special study of inter-cloud flashes. Continuation of study of cloud to earth flashes. | \$ 300 |
| Grant No 100—Judson Daland, Philadelphia Institute for Medical Research, for the study of the function of the Thymus Gland; its influence on growth and development in successive generations of rats. | 2,000 |
| Grant No 101—Everett S Wallis, Princeton University, for the development of methods for the laboratory preparation of oestrus-producing hormones (female sex hormones). | 1,500 |

Grant No 102—T T. Chen, Yale University, for the study of the physical basis of heredity in unicellular organisms. Specific problem: The behavior of chromosomes in <i>Paramecium</i> during endomixis, conjugation and binary fission, in relation to problems of heredity and variations in Protozoa . . .	300
Grant No 103—D. H. Wenrich, University of Pennsylvania, for the continuation of a study of nuclear variations in the parasitic amoebae of man . . .	500
Grant No 104—Louis F. Fieser, Harvard University, for the investigation of the structures of natural products by precision analysis . . .	500
Grant No. 105—Arthur H. Compton, University of Chicago, for the measurement of the ionization produced by cosmic rays in the stratosphere at different latitudes. Measurements are made with instrument-carrying balloons . . .	3,000
Grant No 106—Enos E. Witmer, University of Pennsylvania, for the tabulation and study of the energy levels of the asymmetrical rotator, and the calculation of the magnetic susceptibility of molecular hydrogen by Quantum Theory, using the wave functions of James and Coolidge . . .	200
Grant No 107—J. C. Jensen, Nebraska Wesleyan University, for the investigation of relation of evaporation from lakes and ponds to rainfall from local thunder storms . . .	132
Grant No 108—Herbert H. Whetzel, Cornell University, for the study of the life history and taxonomic studies on the Ciborioideae, a tribe of Discomycetous fungi most of which are parasitic, some of them destructive pathogens of cultivated plants . . .	450
Grant No 109—Modern Language Association of America, Supervisory Committee of Furness Variorum Shakespeare, for the continuation of the Variorum edition of Shakespeare . . .	3,000
Grant No 110—Elsa G. Allen, Cornell University, for the study of the history of American ornithology before Audubon . . .	400

1936, October 9

Grant No 111—Ruth B. Howland, New York University, for the study of reciprocal transfers of imaginal discs between <i>Drosophila</i> larvae . . .	250
Grant No 112—Albert Elmer Wood, Cape May Court House, N. J., for the study of variation among the Cricetid rodents of the White River Oligocene . . .	500
Grant No 113—Joseph Oakland Hirschfelder, Princeton University, for the calculation of the energy of molecular configurations and the ionization probabilities of simple molecules with the aid of the Differential Analyzer of the Moore School of Engineering of the University of Pennsylvania . . .	500
Grant No. 114—Frank Montgomery Hull, Harvard University, for the investigation on the phylogeny and evolution of the Syrphidae based upon fossil and recent genera . . .	300
Grant No 115—Thomas Harper Goodspeed, University of California, for field work in connection with the completion of a monograph of the genus <i>Nicotiana</i> , in which cytogenetic, morphological and distributional evidence will be combined to picture the origin and evolution of the species of a representative genus of higher plants . . .	1,400
Grant No. 116—The Union Library Catalogue of the Philadelphia Metropolitan Area . . .	2,500
(An equal amount was granted by each of the committees on publication and library)	

- Grant No 117—Allan C G Mitchell, New York University, for an investigation of the scattering of slow neutrons with a view to determining more exactly the ratio of the scattering probability to that of capture. 1,000

1936, December 11

- Grant No 118—Davenport Hooker, University of Pittsburgh, for functional and morphological studies of human prenatal development 500
- Grant No 119—Ralph A Beebe, Amherst College, for the direct measurement of heats of adsorption at low temperatures and the measurement of rates of adsorption under accurately controlled pressures of gas 1,000
- Grant No 120—Laurence Irving, University of Toronto, for the study of physiological adjustments of respirations in diving mammals 1,050
- Grant No 121—Robert K Enders, Swarthmore College The mammals of the Chiriqui region of Panama with reference to their distribution, affinities, faunal relationships and life histories, to collect material for anatomical and embryological studies 800
- Grant No 122—Earle Radcliffe Caley, Princeton University, for the application of chemistry to archaeology—the restoration and preservation, chemical examination of ancient objects, etc 2,250
- Grant No 123—Joel Stebbins, University of Wisconsin, for the development and improvement of Photo-Electric Amplifier, application to photometry and colorimetry of stars, study of space-reddening, and of dimensions and constitution of the galaxy 1,000
- Grant No 124—Harold O Burdick, Alfred University, for investigation of the role of the tubo-uterine junction to determine if this region acts like a valve which is directly or indirectly controlled by hormones 500
- Grant No 125—Murray B Emeneau, Yale University, for the continuation of study of Dravidian (and Munda) languages of India 2,000
- Grant No 126—Francis Bitter, Massachusetts Institute of Technology, for the continuation of experiments on the production of intense magnetic fields, and their effect on matter 1,500

1937, February 12

- Grant No 127—James A G Rehn, Academy of Natural Sciences of Philadelphia, for distributional investigation of the Orthoptera occurring in certain areas of New Mexico, Arizona, Nevada and California 500
- Grant No 128—Alexander Weinstein, Columbia University, for a mathematical study of multiple strand crossing over and coincidence in the chromosomes of *Drosophila* 1,500
- Grant No 129—F B Isely, Trinity University, Texas, for the study of the ecology of Orthopterous insects 600
- Grant No 130—Hertha Sponer, Duke University, for investigation of absorption spectra of polyatomic molecules, especially in the photographic infra-red 800
- Grant No 131—Karl F Herzfeld, Catholic University of America, for theoretical investigation of the absorption spectra of organic compounds 1,200
- Grant No 132—William Bell Dinsmoor, Columbia University, for a detailed study of the history, design, decoration and construction of the architectural monuments of ancient Greece in the age of Pericles 1,500
- Grant No 133—Anna R. Whiting, University of Pennsylvania, for a study of genetically different eye and body colors in mosaic males of *Habrobracon juglandis* (Ashmead) 500

Grant No 134—Ralph E Cleland, Goucher College, for the continuation of joint study of the cyto-genetics and phylogeny of <i>Oenothera</i> (<i>Onagra</i>), the evening primrose	1,500
Grant No 135—Rudolf Hober, University of Pennsylvania, for equipment needed in the study of characteristic effects of organic ions on the secretory power of the isolated perfused liver	300
Grant No 136—Albert T Volwiler, Ohio University, for the preparation for publication of the correspondence between President Benjamin Harrison and James G Blaine, his Secretary of State	1,000
Grant No 137—Enos E Witmer, University of Pennsylvania, for continuation of the tabulation and study of the energy levels of the asymmetrical rotator	500

1937, April 9,

Grant No 138—Alexander Goetz California Institute of Technology for apparatus in connection with the investigation of the nature of phase-transitions of small particles of simple substances down to colloidal sizes with special regard to the size dependence of such transitions	1,000
Grant No 139—Gerhard Herzberg, University of Saskatchewan for special apparatus for the investigation of the solar spectrum in the photographic infra-red	1,300
Grant No 140—E J Workman and R E Holzer, University of New Mexico, for the correlation of electrical measurements on thunderstorms with simultaneous photographic measurements for the purpose of analyzing the mechanism of propagation of a lightning flash and studying the electrical structure of thunderstorms	750
Grant No 141—P W Selwood, Northwestern University, for a comprehensive development of magneto-chemistry including the determination of equilibrium constants and activation energies of organic free radical association reactions, continued work on the magnetic properties of rare earth compounds, study of odd-electron molecules, study of the magnetic characteristics of adsorbed gases and their possible relation to contact catalysis	500
Grant No 142—Lester William Strock, University of Oslo, for the study of the geochemical distribution of the chemical elements by means of quantitative spectrum analysis	600
Grant No 143—John H Davis, Jr, Southwestern College, for the study of land building as influenced by mangrove vegetation in south Florida and adjacent waters, the geologic role of mangroves	350
Grant No 144—Albert Tyler, California Institute of Technology, for the investigation of the action of various metabolic stimulants and depressants on the rate of respiration and development of eggs of marine animals	300
Grant No 145—William R. Amberson, University of Tennessee, for the study of the behavior of the mammalian body when its normal blood colloids are replaced by gum acacia, the determination of the inter-relationships between the various colloids in the blood stream during the period of recovery from "total plasmapheresis",	250
Grant No 146—Alfred Chanutin, University of Virginia, for the study of renal insufficiency as produced by partial nephrectomy	1,000
Grant No 147—Judson Daland, Philadelphia Institute for Medical Research, for the continuation of studies, through succeeding generations, of the role of the thymus in the rate of growth and development of the young	2,000

- Grant No. 148—Rudolf Höber, University of Pennsylvania, for the investigation on the isolated surviving liver, which organic substances are appropriate to promote, and which to diminish, the normally existing secretory power of the liver with respect to the bile-pigments and other dye-stuffs 1,200
- Grant No. 149—Frederick Edward Braach, Library of Congress, for the study of (1) the history and progress of scientific thought in the American colonies, 1636-1783, (2) the rationalizing influence of the Royal Society and Sir Isaac Newton, (3) centering in the lives of John Winthrop (1714-79) and David Rittenhouse (1732-96) 600
- Grant No. 150—W. Norman Brown, University of Pennsylvania, for the archaeological excavation at the prehistoric (3d millennium B C) site, Chanhu-daro, Nawabshah District, Sind, India 3,000
- Grant No. 151—The University Museum, University of Pennsylvania, for the seventh field season of the Museum's excavations at Piedras Negras, Guatemala 3,000
- Grant No. 152—Alfred J. Swan, Swarthmore College, for the permanent preservation of wedding rite and folk-songs in the ancient Russian district of "Pechory" now in Esthonia 250

The distribution of these grants to the various fields of learning is shown in the following table.

Field	Grants	Amount
Astronomy	2	\$ 2,300
Physics	9	10,200
Chemistry	5	5,250
Geochemistry	1	600
Meteorology	3	1,182
Paleontology	1	500
Botany. . .	3	3,350
Ecology	1	350
Zoology	11	6,150
Physiology	8	8,100
Anatomy	1	500
Philology	1	2,000
History	2	1,600
Archæology	3	7,500
Literature	1	3,000
Music.	1	250
Union Library Catalogue of the Philadelphia Metropolitan Area	1	2,500
Total	54	\$55,332

There has been no attempt to equalize the amounts granted in these fields, since the needs are not the same in all subjects, but the Committee does desire to distribute grants to the various fields of learning in accordance with needs and the probability of valuable results.

Owing to the fact that payments on grants are usually made quarterly or only as needed, it happens that considerable sums that have been assigned to applicants are held in the treasury of the Society until they are called for. This leaves the care and investment of these assigned sums to our Treasurer rather than to the applicants and it sometimes tends to encourage their prompt prosecution of work and their filing of reports of expenditures and of progress. Such *ad interim* reports of progress are usually brief and in no case is it intended that they should be burdensome. When a research for which a grant has been made is far enough advanced to warrant it, a report or at least an abstract is expected for publication in our *Proceedings*, and some researches which are of marked scientific value or of general interest may be presented to the General Meetings of the Society. At the Autumn General Meeting on November 25 and 26, 1936, 17 papers presented were by recipients of grants and a number of papers at the Annual General Meeting in April are of this nature. To be asked to present a paper on such an occasion may well be regarded as a distinguished honor, and it is generally so regarded by our grantees. On the part of the Society there can be no doubt that our programs and publications have been enriched by many of these reports. The program of the Autumn General Meeting on the two days following Thanksgiving Day 1936, was largely composed of such reports, and it was the general opinion of those present that it was a very successful meeting and that such Autumn Meetings should be continued in the future.

The total number of reports, papers and monographs based in whole or in part upon work aided by grants from the Penrose Fund is difficult to determine but is in the neighborhood of 120. Of this number some 38 have appeared in our *Proceedings* and *Transactions*, and 27 in *Miscellanea*.

In the report of the Committee last year it was suggested that "our present plan of making grants for research should not be regarded as permanently fixed. We should continually study to find the best means of promoting knowledge and the

Committee on Research will welcome suggestions as to feasible ways of improving this work of the Society." In furtherance of this study of the best means of promoting research the Society sponsored a meeting at its Hall on February 19 and 20, 1937, of representatives of some of the leading organizations engaged in administering funds in aid of research. Some thirty-five organizations including research foundations, institutions, societies, councils and universities were represented by officers or members of staff and most of these took part in the round table conference on February 19 or in the open session next day. Some of these organizations have had many years of experience in this work and their contributions to the meeting were most helpful; others more nearly approached in means and procedure our own Society and their experience was of especial value to us. It is impossible in this report to summarize the various views presented, but these are being published in an accompanying number of our *Proceedings* and will thus be made available to all who are interested in the subject. No resolutions were proposed and no attempt was made to bring about uniformity of methods but it is safe to say that by this conference a beginning has been made in the cooperation and correlation of various agencies engaged in promoting research. While the funds for research at the disposal of the American Philosophical Society are much less than those of some of the great foundations and universities they are greater than those of many other organizations. While we cannot compete with the great foundations and universities in organizing and supporting great research projects or in maintaining research professorships and fellowships, we are able to award grants of a larger size than can be given by research councils and many other organizations. There was naturally some difference of opinion as to the relative need and value of fellowships as compared with grants-in-aid, but the general conclusion was that grants-in-aid could be made to benefit a much larger number of investigators than could fellowships and that the need and value of such grants was very great. It was the

general conclusion of many who were consulted that the American Philosophical Society has made no serious mistake in its plans and procedures for promoting research and, on the contrary, that it has taken an important place among the institutions that are administering funds in aid of research.

From its foundation to the present the essential work of this oldest learned society of America has been threefold:

- (1) The stimulation of intellectual and social contacts among scholars in all fields of learning by means of meetings and correspondence;
- (2) the diffusion and conservation of knowledge by means of publication of scholarly work, exchanges with other societies and the building up of a library;
- (3) the increase of knowledge by the only method by which it can be increased, namely research.

These are the ways by which the American Philosophical Society can fulfill the purpose of its founders in "promoting useful knowledge,"—meetings, publications, research,—and the greatest and most fundamental of these is research.

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